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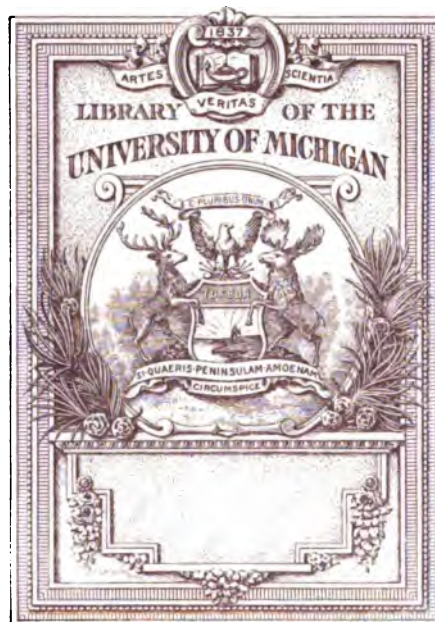
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THE ANALYSIS OF RACIAL DESCENT IN ANIMALS

BY
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*In Memory of
a Wise and Tender Father and
a Noble Gentleman*

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kind of the stimulus is known, and in this way complex associations be split into simple components.

If one should limit himself to the strictly experimental method, however, he would be neglecting an enormous range of phenomena. For living organisms are in number and variety hardly commensurate with the vast assemblage of their ancestors. Are we then to leave out of consideration all this once existing life, simply because its units are no longer subject to experiment? Most assuredly not. And this is the greater part of the ground of the study of racial descent, known more concisely as phylogeny. The study of genetic relations of organisms has always impressed itself as a source of great interest, ever since the idea of the mutability of species became founded. We should not mentally separate modern organisms from those that have become extinct, and without some idealization of the latter we can form no adequate conception of the former. For all the explanations of the biologist are interpretations of genesis, whether he considers a race, an individual, a part or a habit.

This study of phylogeny has come into a certain disrepute amongst superficial thinkers who imagine that there can be no certainty in its conclusions. And it must be admitted that the work of many phylogenists has been unscientific in the extreme. But one should not attack a line of research because some of its followers are at fault. One should judge rather by its positive contributions, and so doing will find that many of the broader concepts of biology have been attained from just such investigations. As to the degree of uncertainty in its conclusions, this results simply from the great extent of the phenomena to be explained and from their complexity. Biology is less precise in its formulations than physics or chemistry because its scope is so much greater; and for the same reason phylog-

eny is less exact than other more narrowly circumscribed paths of biological inquiry. Just because the field is so full of tares, the more reason to till it.

It seemed unnecessary to present any historical account of the systems of classification that have been from time to time put forth, for summaries of them have frequently been given, as notably those of Spix (1811), Carus (1872), and Louis Agassiz (1857), and I have no schemes of classification to offer, but only a discussion of methods and of phenomena.

The argument is from the side of Zoology, because I have more acquaintance with the phenomena of animals than with those of plants.

So far as possible I have duly accredited previous opinions and ideas, striving to name the first presenter of them, or the principal founder, and not to give complete historical treatments. The method most in use among zoologists has been followed, in referring to a particular book or memoir, of bracketing in the text immediately behind the name of the writer cited the date of publication of the work in question. At the end of the book is the literature tabulation, where the list of authors is alphabetically arranged and, in case more than one work of an author has been cited, his several works are arranged in sequence of publication. This method saves many foot-notes in the body of the text; and the literature list is at the same time a convenient index of the authors referred to.

For friendly criticisms upon certain points I am indebted to Professors Thomas H. Morgan, Herbert S. Jennings and William M. Wheeler.

THE UNIVERSITY OF TEXAS

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THE ANALYSIS OF RACIAL DESCENT IN ANIMALS

CHAPTER I

ENVIRONMENTAL MODES OF EXISTENCE

THE earlier study of geographical distribution of organisms has within recent time greatly extended its scope and enlarged its methods, so that it has become a most important method of analysis of lines of descent. Naturalists failed to note its value so long as they applied themselves merely to the older geographical cataloguing of animals and plants, and failed to broadly consider the fundamental environmental conditions of life. The subject indeed has grown so, that we might well include under it all the habit phenomena of organisms, all their modes of behavior and response, so far as they are not limited to activities of protoplasmic particles, and to take in the whole series of phenomena called variously ecological and ethological.

A. HISTORICAL AND INTRODUCTORY

To better understand the present scope of the subject it is well to consider its history.

The study of geographical distribution is comparatively young. A. Wagner (1844) was the first zoologist to take up the subject, and was followed by Dana (1853) and Schmarda (1853). For nearly three centuries previous great collections of exotic animals were coming into the European museums from Africa, America and the East Indies, and the nature of these animals showed that life differed in different parts of the Globe, and that particular

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species are more or less limited in their dispersal. Naturalists were so much occupied in the description and classification of the new forms, that for a long time they paid little attention to questions of distribution. When they did commence to do so, they compounded a zoological geography, arbitrarily selecting particular regions of the world and characterizing them by the animals and plants found there. As Ortmann (1896) observes, the early study was "a purely descriptive science, based on empirical facts, without the attempt or wish to explain the causal connection of the then known facts." The idea of transmutation of species, also, had not yet been forced upon men's convictions, so that the attitude in that day is well represented by Louis Agassiz (1857): "It appears to me that as the facts point now distinctly to an independent origin of individuals of the same species in remote regions, or of closely allied species representing one another in distant parts of the world, one of the strongest arguments in favor of the supposition that physical agents may have had a controlling influence in changing the character of the organic world, is gone for ever." But Forbes (1843, 1846) attempted to relate modern distribution with geological past; Dana considered the factor of temperature; and Mosely (1855) distinguished in the sea between pelagic, littoral and abyssal modes of life.

The earlier writings were, however, mainly catalogues of animals found in arbitrarily defined regions; and many later attempts, even some of those of the present time, have not advanced beyond them in scientific value, because they disregard the most fundamental of the environmental conditions.

Sclater in 1858 published a memoir upon the distribution of land Birds that was of importance because of its great influence upon so much of the later work of the kind. That

is, the larger terrestrial regions recognized by Sclater, the Palaearctic, Ethiopian, Indian, Australian, Nearctic and Neotropical, have been accepted (with only two important modifications) by most subsequent students of Birds and Mammals. Sclater disregarded the political and continental subdivisions of the Globe, and defined his large "regions" on the occurrence of certain groups of Birds. He selected the particular Bird groups entirely arbitrarily, however. Murray (1866) went further, in considering geological change and barriers to dispersal. But the great basis for all later work upon the distribution of Birds and Mammals is the monumental book by Wallace (1876). This is a mine of statistics upon the distribution of each family, in many cases of the genera also. But much more than this Wallace was the exponent of transmutation; he showed the necessity of understanding the distribution of ancestral fossil forms and of knowing geological change, and he investigated in detail the modes of dispersal and the barriers to it. Lamarck was led to the idea of transmutation from the geological standpoint, Darwin from the analysis of domestic races, Wallace from the study of distribution. This is without doubt the most important monograph upon distribution, though some of its conclusions are traceable to Sclater, Murray, and Rütimeyer.

Günther (1880) compared for the Fishes the influences of fresh, salt, and brackish media; he considered both climatic and topographic relations of the environment, and distinguished between ancient types (relicts), indigenous or autochthont forms, and immigrants. This book and an earlier one by Alexander Agassiz (1872) give the first broadly scientific exposition of marine distribution. The considerable value of the work of Heilprin (1887) is that he considered conjointly all groups of animals, all environmental zones, and paid attention to geological distribution.

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Simroth (1891) has maintained an entirely new point of view. He also comprehends all the groups of animals, even the main groups of plants, and particularly from data of general physiological phenomena, such as respiration, nourishment, locomotion, skeletal structure, etc. This book is an entirely new departure, in attempting to define not environmental regions of a geographic kind, but rather environmental influences, and is a study of the influences upon structure of the land, the sea, and the freshwater. Two important recent studies, by Walther (1893) and Ortmann (1896), mark a great advance in the interpretation of the factors of marine distribution. It should not be forgotten that the modern treatment of environmental influences in its bearing upon distribution owes much to the classical little book of Sémper (1880), on the "Natural Conditions of Existence of Animals"; and the botanical treatment of distribution preceded the zoological, and for a long while influenced it. But the present phase of botanical study of distribution is for the most part not interpretative, not scientific, but rather a mere cataloguing of plants found upon particular soils, in particular degrees of temperature and moisture; it pays little attention to geological distribution and racial descent.

This gives but a brief summary of the progress in the subject and many important papers could not be mentioned; but it is sufficient to show how the point of view has changed. The first work was upon Birds and Mammals, and to this day these groups have received disproportionate attention. First with the great oceanic dredging expeditions, of which the British "Challenger" expedition has been the most fruitful, and the work of A. Agassiz and Hensen, marine distribution came to be better understood. More recent still is our knowledge of the freshwater life. Even now there have hardly been accumulated data suffi-

cient for comprehensive treatment of all groups, for only a few are sufficiently well known. Thus there has not been a beginning made in the matter of the distribution of the insects.

The study of distribution has at last become a scientific one, one seeking reasons. The days of the older zoological geography are passing, and, but more slowly, the idea that provinces mapped out for a particular group of organisms will hold for another one. It is now a question of environmental distribution, not geographical. In defining life zones it is not a problem of what diverse animal groups have coterminous geographical boundaries, not a question of haphazard sorting of numerous isolated data of special cases of distribution. We could no more get a science of distribution by a compilation of geographical distributions of various groups, than a scientific phylogeny of a group of animals by a compilation of a lot of schemes of classification, based each upon a separate structural character. Yet too many attempts of the present time seem ignorant of this, and continue to maintain that such elaborations are really scientific and not mere catalogues of facts. Further, a little thought makes it evident, as particularly Simroth, Walther and Ortmann have argued, that no single environmental factor can be taken as a basis for the interpretation of distribution, but that all the principal conditions regulating existence and dispersal should be considered. Thus a treatment with respect to temperature alone as that of Merriam (1894) is clearly deficient in proportion to the number of factors it disregards; equally unsatisfying is any one that fails to take into account the genesis and change of present physical conditions.

Scientifically treated, environmental distribution is the analysis of centers of origin of species and higher groups, and of their dispersal from these centers, both considered

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in the light of environmental stimuli and conditions. This means an understanding of geological changes so far as they affect the habitable regions of the Earth, of the paleontological succession of life, but most particularly of the present conditions determining existence and producing transmutation. The problems are indeed broad enough, it is a jungle of problems.

The method should be to start with some small restricted group of diverse distribution, preferably one represented in different media and in manifold environments. The Amphibia, various Crustacean groups, Gasteropod Molluscs, Turbellaria, all these are examples that promise much. For a strictly terrestrial group sheds no light upon an aquatic one, nor one limited to the sea upon freshwater existence. By the careful analysis of what factors have brought about the present distribution in each of such various cases, there can gradually be reconstructed a comprehensive understanding of environmental factors and their relative importance, as well as a completer knowledge of transmutation. And, as is always the case when the method has been consistent and scientific, the factors of distribution and the meaning of it will ultimately be stated in very simple form. These factors appear to us now to be enormously complex, but this is because we have hardly commenced to analyze them. We have to study environmental action and not geography.

B. MODES OF EXISTENCE

Our object is to see what bearings and what value the study of environmental distribution has upon the determination of lines of descent. And just because we are employing characters of distribution to help explain racial descent, it is quite obvious that we must avoid the *circulus*

vitiosus of seeking to explain distribution in the light of any preconceived views upon the phylogenetic relationships of animals. There is some basis for the general assumption that two species will be found dissimilar, if they live far apart, or under different conditions; and phylogenists generally recognize that facts of distribution are of importance in determining degrees of relationships.

Three main assemblages of organisms are commonly distinguished with regard to the media in which they live: the terrestrial, freshwater and marine, for which Haeckel (1890) has proposed the respective substantives *geobios*, *limnobios*, and *halobios*. Because the medium represents very fully the environmental conditions of existence, this is a very satisfactory classification of such organisms as are restricted to the atmosphere, to freshwater, and to the sea. And using the term *geobios*, or the adjective *geobiotic* or *terrestrial*, we should bear in mind not the earthly substratum but the enveloping atmosphere, because the bottom of the sea or of a lake is also earthly. But there are two other bionomic groups that should equally well be distinguished, as we shall try to prove, and these groups demarcated likewise by characters of the medium.

In the general usage of the word such animals as Tapirs and Beavers are called *amphibious*, since they live partly upon water and partly upon the land; a Seal or a Manatee or a Snake is in the same way called *amphibious*. But there are other animals which are *amphibious* in quite another way, in passing one stage of their existence in one medium, and another stage in another medium. So the tadpole of a Frog and the larva of a Mosquito live in water, the adults of both of these species upon the land. There are then two kinds of *amphibiousness*. Some animals during their whole existence may live interchangeably upon land or in water, other animals are at one stage restricted

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to one medium, at another period to a different one. The former can be easily classed as either aquatic or terrestrial, according as to whether the sum total of their characteristics seem better fitted for aquatic or for land life. Thus a Tapir or a Hippopotamus is essentially terrestrial, while a Seal or a Manatee, and to less extent a Beaver, is essentially aquatic.

But it is otherwise with the second group of animals mentioned, those which live during a particular period in one medium, then later in their lives migrate into a different medium. A Mosquito or a Toad is neither strictly aquatic nor strictly terrestrial: one stage is a complete adaptation to water, its existence then is possible only in this medium, but as an adult it can live only in the atmosphere. Because such existence implies profound change of a bionomic nature during the course of the individual's history, and because this is a relatively rare condition, animals that possess it should be regarded as a separate and well marked bionomic class, to which the name *diplobios* may be given.

The alternative would be to classify this *diplobios* as either aquatic or terrestrial, according to the nature of the environment during the adult stage, or according to the relative amount of time spent in each particular medium. But this alternative is unsatisfactory just because it fails to indicate the essential bionomic peculiarity, the complete change of medium at a particular embryonic period. The *diplobios* as just defined would include all organisms, excepting the endoparasites, that at different periods of their existence occur in any two of the three media, air, freshwater or salt water. Most combine freshwater and terrestrial life, and the most numerous examples occur in the Insects and Amphibians. A much smaller number combine terrestrial and marine life, such as the great Sea Turtles

and some Crustacea. An equally small number combine marine and freshwater existence, such as the Eel and the Salmon. This would seem to show that there is a closer resemblance between freshwater and terrestrial conditions, than between those of land and sea, or freshwater and sea, a point to which we shall have occasion to return.

But still a fifth bionomic group has to be distinguished, namely those animals that at some period of their existence live as internal parasites. This one differs more from the other bionomic groups than do any of the latter from each other. So it is entirely unreasonable to hold, with Ortmann (1896), that entoparasites should be classed with their hosts, because an entoparasite has an environment and mode of life entirely different from that of its host. The greater number of animal internal parasites live within other animals, a smaller number (as gall-forming Insects) within plants; and the former became more secondarily modified than the latter. All entoparasitic Metazoa have one period of free existence; this is usually, when they live within other animals, during the earliest portion of their development and is generally aquatic, more rarely (Gordiacea) is the end stage also free. But the majority are entoparasitic for the greater portion of their lives. Accordingly, though they have a double existence, with a change of medium at a particular period, they should not be grouped with the diplobios in which all stages are free. The essential peculiarity of this *entobios*, as it may be called, is that during a great part of the existence the environment is wholly an organic one, and that the animals are enveloped by some substance of the host, and not by pure water or pure air. It is indeed remarkable that students of environmental conditions should have failed to dignify the entoparasites by a particular bionomic group name. Their medium is organic and living, very different

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from the media of water or air. To say that an internal parasite of a Shark should be considered with the host as a marine organism and nothing else, is simply to leave out of count the whole nature of the environment of the parasite.

Ectoparasites, on the other hand, while dependent upon hosts for nourishment, live in the same medium as the hosts, and so may well be classed with the latter. Because entoparasitism has been evolved out of ectoparasitism, so that entoparasites are simply more advanced parasites, is no reason from a bionomic point of view for regarding all parasitic modes of existence as essentially similar, and for regarding ectoparasites and entoparasites as constituting one and the same mode of existence. For a Seal is essentially marine, and we call it so, though its ancestors were terrestrial. Related to ectoparasitism is commensalism, where diverse species live in association to their mutual advantage; and social parasitism, as in the relations of Ants to Aphids, and of one species of Ant to another. The genesis of all such states is an important problem, and its analysis can throw much light upon the genesis of habits and thereby of species also. But it is our intention here to draw consideration only to the major conditions of life.

Accordingly, in addition to the geobios, limnobios and halobios, two other modes of existence should be recognized, namely, the diplobios and the entobios. The environmental characteristic or principle employed throughout in the definition is the medium. The first three may be grouped together as monobios, that is, life without change of medium; while the entobios and the diplobios have in common existence with change of medium, and together may be said to constitute a heterobios. This heterobios has, of course, a more complex existence than the monobios.

These fundamental modes of existence have each a par-

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ticular environmental medium, and these media constitute the primary bionomic regions; all of these regions may occur in close proximity to each other and even within a restricted geographical area, as upon a sea coast. We need not consider the subdivisions of the entobios. The kinds of the diplobios would be the various combinations: geobios and limnobios, geobios and halobios, limnobios and halobios. To decide what are the main subdivisions of the three other three modes of existence, it becomes necessary to determine what are the other main conditions of life besides the medium.

Semper (1880) mentions as main influences in the non-living environment: nourishment, light, temperature, stable water and stable atmosphere. Ortmann (1896) has insisted upon another important agent, the substratum, which may be either land (wet or dry) or water; as the bases of bionomic subdivisions he regards this substratum, light and medium. There can be no question of the importance of the condition of the substratum, because it determines two important vital processes, nourishment, and the active means of securing food, locomotion. Light is quite equally important, because it is an absolute necessity of plant life and animals are dependent either directly or indirectly upon plants for food. Walther (1893) had previously called attention to the importance of light as a factor in distribution, and he named *diaphanic* all environment penetrated by light, and *aphanic* all environment beyond its influence; we will use these adjectives for the organisms as well as for the environments. Temperature is much less important than either of these, yet sudden change of temperature is a powerful barrier to dispersal. In other respects temperature affects animals mainly by influencing their food supply. Students of the geobios have placed an exaggerated importance upon temperature influence.

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If we now employ the conditions of light and substratum we would attain the following subdivisions of the geobiotic, limnobiotic and halobiotic conditions of existence, as pointed out particularly by Ortmann. Geobiotic is the existence either (1) under the influence of light, diaphanic, or (2) beyond the region of light, aphanic, the latter condition is rare, and would correspond to life in subterranean regions not penetrated by light. The substratum in both of these is more or less dry land. The halobiotic environment is (1) diaphanic, that is, the sea water as far from the surface down as light rays penetrate, about 400 m., and so far as plant life extends; and (2) aphanic, the region beyond the influence of light, what is generally known as the abyssal, all the sea from a depth of about 400 m. below the surface down to the bottom, characterized also by very low temperature and absence of plant life. The diaphanic halobiotic region has been well divided by Ortmann, on the basis of the substratum, into two environments: (a) the littoral, where all life is to greater or less extent dependent for food upon the sea bottom, therefore the bottom life from the beach level down to a depth of 400 m. from the sea surface; and (b) the planktonic, all that water in which occur animals not dependent upon the sea bottom for food, characterized by pelagic life or plankton, life for which the substratum is then water and not ground. Ortmann has defined the littoral and the planktonic life differently from his predecessors, in considering primarily the nature of the substratum. And the littoral, as defined by him, includes all marine life within the influence of light dependent upon the sea bottom for food; that is, much life beyond that of the shore. The freshwater existence can be subdivided in the same way as the marine, into a (1) diaphanic, with the subdivisions of the littoral and plankton or pelagic, and (2) an aphanic, which would include the great depths of lakes

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below the influence of light, as well as subterranean fresh waters excluded from the influence of light.*

Such modes of existence can be tabularly represented as follows:

Heterobios	{	Entobios		
		Diplobios		
	{	Geobios	{	Diaphanic
				Aphanic (subterranean)
Monobios	{	Halobios	{	Diaphanic
				Aphanic (abyssal)
				{ Planktonic
				Littoral
	{	Limnobios	{	Diaphanic
				Aphanic
				{ Planktonic
				Littoral
				{ Abyssal
				Subterranean

With regard to their habits of securing food organisms can be classed as sedentary (sessile) and locomotory; the latter change their position actively, by movements of their own, or passively, by movements of the surrounding medium. No animals are sedentary at all periods of their existence. Most of the terrestrial plants are sedentary, none of the terrestrial animals are, and it is a relatively small number of non-parasitic aquatic animals that are sessile. There can be no doubt that the sedentary condition is a secondary one, and therefore, as particularly Lang (1888) has pointed out, that structural peculiarities of sedentary animals, such as radiality, are secondary and not primitive features of them.

* Haeckel (1890) classifies the life of the sea as (1) the benthos, the life on the bottom, (2) the plankton, the pelagic life as we have used the term, and (3) the nekton, by which he denotes swimming organisms that depend upon the bottom for food. But it seems better, with Ortmann, to distinguish in the benthos between the life of the abysses and the life within the action of light, and to call all animals bottom forms (benthos) that are dependent upon the bottom for food, whether they be sedentary, vagile, or temporarily nektonic (swimming).

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C. GENETIC RELATIONS OF MODES OF EXISTENCE

Now we come to the question of immediate interest, the relations of these main life modes to each other, and the question of which of them is the most ancestral. The entobios can be disregarded as being manifestly a very modified kind of existence, and the diplobios because it is also a union of two modes of life. Which is the most primitive, the geobios, limnobios or halobios?

It is usual in such problems to project the imagination into earlier times, to try to decide what were the physiological conditions of the surface of the Earth when it first became habitable. The nature of subsequent geological changes has been to some extent empirically determined, such as upheaval of the sea bottoms and their subsidence, with the consequent changes in relative amount and configuration of the dry land; the lines of volcanic eruption, the erosion of land exposed to atmosphere and frost, and the relative time and extent of more recent glacial epochs. There is even some evidence that seasonal climatic change has not existed from the beginning, but that originally all the surface of the Globe experienced uniform climatic conditions, or at least uniform temperature.*

On the old hypothesis of Laplace and Kant the Earth has been cooling gradually since the time of its first formation, the atmosphere also freeing itself of gases and depositing these substances upon the surface of the Globe; a recent geological hypothesis is that the internal temperature of the Earth has been steadily increasing as a consequence of increasing pressure from the surface. Life could not have

* There is, however, much conjecture in all this, particularly with regard to the factors initiating climatic seasons, as one finds in comparing the ideas of Neumayr (1887), Heilprin (1887), Geikie (1893), and the older work of Croll (1875).

existed until water had condensed on the surface of the Earth, and until the atmosphere became transparent to sun rays. The general opinion of geologists seems to be that the earliest seas, on account of their higher temperatures, held more substances in solution than do modern ones. From such a point of view the earliest waters should have been the most saline. So Geikie states (1893, p. 35), "Under the enormous pressure of the primeval atmosphere, the first condensed water might have had a temperature little below the critical one. In condensing, it would carry down with it many substances in solution. The salts now present in sea-water are to be regarded as principally derived from the primeval constitution of the sea, and thus we may infer that the sea has always been salt. It is probable, however, that, as in the case of the atmosphere, the composition of the ocean-water has acquired its present character only after many ages of slow change, and the abstraction of much mineral matter originally contained in it. There is evidence, indeed, among the geological formations that large quantities of lime, silica, chlorides and sulphates have in the course of time been removed from the sea."

With respect to this point Simroth (1891) has to say: "Should it be capable of proof that all water, even the ocean, were originally fresh, we should have won thereby an extremely valuable point of view, from which we might enlarge that from the freshwater had branched off to one side the marine, to the other the land fauna. We shall see that many facts point to similar significance of the freshwater, and that it in many ways has occupied such an intermediate position in the history of creation." But following the accepted geological view he argues against a "salt-free primeval sea." More recently Moore (1903) has discussed the same question on the basis of an interesting study of the modern fauna of Lake Tanganyika. This particular body of

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water is now fresh and without oceanic connection, but with evidently archaic Gasteropods since their closest relatives appear to be fossils of the Jurassic period.

Now the moisture of the modern atmosphere is water derived by evaporation from the sea; condensing it falls upon the land in the form of rain, and so supplies the rivers that empty into the sea. As far as we know (*cf.* Walther, 1893) the total amount of water of the Globe may have remained the same during all geological history, and have varied only with regard to its chemical condition. Rain is nearly chemically pure water, containing only a minute amount of substances derived from the atmosphere. But on reaching the surface of the Earth it dissolves many substances, is probably in fact a universal dissolvent, and carries with it such materials to the sea. Because such material is not removed from the sea by the evaporation of its surface water, it follows that modern seas must be getting more concentrated in solutions, or at least be kept at a degree of saturation beyond which solutions become sedimented. This suggests that modern seas may be fully as saline, or nearly as much, as they ever were. It is possible that they were super-saturated in the early times of their high temperatures, then on cooling sedimented much of the contained material so as to become nearly fresh, later by the constant inflowing of saturated freshwater together with the evaporation from their surfaces became again highly impregnated. But so long as there is no positive proof against the assumption of the high temperatures of the primeval seas, we have no good geological basis for concluding that these seas were ever fresh. The case of Lake Tanganyika is not really contradictory. This might have been originally connected with the ocean, then have become cut off from it; but that ocean may have been salt, and the Lake have become fresh secondarily.

However, at the present time all is conjecture concerning the nature of the early seas; there is no good foundation for any one of the particular views. And there is but little more evidence for the conclusion that the early seas were shallower and more extensive. Thus geology does not help us out in the question of whether saline life is more primitive than freshwater life. And indeed we might almost say that the study of environmental distribution of animals has been of more help to geology, than geology has been to it.

An argument for the primitiveness of the freshwater life has been based upon the phenomenon of the wide distribution of many freshwater species, identical species, particularly among Protozoa and Rotatoria, being found in widely separated bodies of freshwater, in lakes and rivers that could never have been connected. This phenomenon is one of the reasons why the faunistic examination of the freshwater has been so long neglected: observers in different parts of the world found closely similar freshwater species, and nothing like the wealth of different species that are found upon the land or even in the sea; there was missing the stimulating expectancy of new species. It has also been argued that such wide dispersal of these identical freshwater species points to their great age. But it is notable that it is particularly members of the Protozoa and Rotatoria that show the power of encystment, an adaptation against evaporation, consisting in the formation of exudate cysts at the time when the surrounding water dries up. These mostly minute organisms can be transported enormous distances in the encysted condition, by the agency of wind and other means. Wallace and Darwin have demonstrated how many modes of carriage there are for such beings. The greatest barrier to their dispersal seems to be sea water, but some may even be transported without injury by the oceans, and thereby have the chance of being

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cast upon a distant sea beach, and ultimately reaching freshwater again. Accordingly, wide and separated distribution of freshwater organisms is no proof of their primitiveness or age, but rather of their adaptability to passive transportation. Some freshwater animals, as notably Newts and Fishes, cannot be passively carried about by the air or across salt water, and they show consequently far less extensive geographical ranges. Freshwater conditions on the whole appear to be more alike the world over, than do oceanic conditions where the environment is larger and more diversified; this would be partially explanatory of the general similarity of freshwater faunae.

Simroth (1893) has ably and eloquently reasoned that the line of the sea beach, from the region of high tidal limit to a short distance below the low tidal, is the probable point of origin of most animal groups, because it includes the most diversified environmental conditions. As Simroth states, this is the meeting place of sea, land and freshwater, and here the conditions would be most stimulative to transmutation. He argues that from this region has originated in one direction the pelagic, littoral and abyssal fauna of the sea, in the other the fauna of the land and the freshwater. From a variety of considerations he reasons that many more groups have had a terrestrial origin than is generally supposed, as for instance the Fishes and Crustacea, even perhaps the Molluscs and Annelids. He states that iron is found not in the sea, but only in freshwater and upon the land, and argues that all organisms containing iron compounds could not have originated in the sea. And further, he reasons that no forms with heavy external skeletons, nor such with jointed appendages, could have acquired these structures in deep water, because they would be hindered in swimming by their weight; they could have developed them only in conditions of the shallow water or

of the atmosphere, and primarily as a protection against the latter. Simroth has brought together a great series of facts, hitherto disregarded by students of distribution, and though there is a degree of wildness in some of his expositions, his ideas command careful regard. He considers that the land close to the sea, and the shallow water of the sea near the land, was probably the ancestral home of most groups of organisms.

The prevalent view is quite different from this one, it is that the pelagic oceanic life is the primitive one, from which later the bottom of the sea became peopled, when the plankton "discovered the bottom" as Brooks (1893) puts it; while from the bottom life of the sea margin the land and the freshwater became inhabited. Few have ventured to oppose this idea, first suggested by Murray (1866), yet certain considerations show that it is hardly probable.

Of the bionomic regions of the sea the abyssal may be neglected as a primitive center of life, because it has the least heat, no light and no vegetation, and a paucity of animal groups. Of all habitable environmental regions it seems the most inhospitable. We have to compare next, then, the pelagic and the littoral faunae.

The number of strictly pelagic marine groups is relatively small, of groups which are not at all dependent upon the sea bottom but live always suspended in water. These are among Protozoa the Radiolaria and some Foraminifera; among Metazoa the Ctenophora, Chaetognatha (*Sagitta*), various Medusae, the Siphonophora and Copepoda, and among the Tunicates the Salpae, Appendiculariae and Pyrosomidae, and that most interesting of all animals, *Doliolum*. All the other marine groups are dependent for at least some portion of their existence upon the sea floor, so most of the Protozoa, Hydromedusae and Scyphomedusae, all the Anthozoa, Echinoderms, Annelids,

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Dinophilus, Sipunculi, Bryozoa, the greater number of the Turbellaria, Nemertini, Crustacea, Tunicata, Nematoda, Mollusca and Fishes. The fauna restricted to those floating sea-weeds constituting the Sargasso-sea is strictly not pelagic but littoral, since this vegetation is a detachment of the littoral flora. The preponderance of groups of both animals and plants is in favor of the littoral, bottom life, whether the species be attached to the bottom, creep upon it, or swim about it.

Then the environment of the plankton is very monotone, compared with the littoral, with less variable conditions of stress and strain, of change of temperature and water constitution, with far less variety of plant life. But the life of the sea bottom within the influence of light, and particularly that portion of it beneath shallow water and near the shore, presents the greatest variety of food both organic and inorganic brought down by the rivers and carried in by the wind and tides, while the farther the sea water is from the bottom and from the shore the purer is it and the freer from contained food substances. The greater diversity of life is associated with these more diverse and favorable environmental conditions, and we are justified in concluding that these conditions have been the principal cause in indirectly bringing about the manifold transmutation of that life. The monotonousness of the pure water of the high seas offers far less stimulus to transmutation.

The characteristics of the plankton are also not necessarily primitive. A Siphonophore is a colony of individuals which are reduced to the value of organs, an asexually produced stock. But such stocks are characteristic particularly of bottom, sessile organisms, and for this reason a Siphonophore as well as a *Salpa* could better be regarded as a bottom form which has later become floating, than as a form that had always been pelagic. Most pelagic ani-

mals have hydrostatic apparatus developed in various ways, organs to keep them afloat and to aid them in their vertical migrations. But these are relatively complex structures for the most part, they could not have been present from the start, could not have been possessed by the ancestors, and therefore their ancestors could not well have been pelagic. We generally think of the Medusae as both primitive and pelagic; but the sessile Polyp is simpler in structure whether it is more primitive or not, and certain Medusae, as *Gonionemus*, crawl about by means of their tentacles upon bottom plants. The same general argument will apply to the animals of the freshwater, where those that are pelagic are, on the whole, decidedly more modified and less numerous than those of the bottom.

All these are reasons, without any great weight to be sure, but still quite as strong or stronger than those of the more prevalent view, to show that in general existence upon and around the bottom within the influence of light is to be regarded as more primitive than planktonic life. Most of the modern marine animal groups are littoral, and there is some reason to hold that the ancestors of the pelagic forms were littoral also, and that the latter are secondary modifications. It is particularly the diversity of the littoral environment that would be a powerful stimulus in the transmutation of species.

In another chapter it will be shown that the existence of freely motile larvae in many marine groups is no argument at all for the pelagic origin of these groups; yet that has been the main argument of those who conclude the pelagic mode of life to be the ancestral one.

So our problem is narrowed. The abyssal and planktonic life of the sea, the entobiotic and diplobiotic life, none of these can be rightly considered primitive. The planktonic and abyssal life of the freshwater can also be disre-

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garded, and for the same reasons that decide us to omit the corresponding existences in the sea.

We inquire then: which kind of life is probably the most ancestral, that of the land, the littoral limnobios, or the littoral halobios? There is this environmental community of the three, that the organisms in all are dependent for food upon a substratum of earth, while the difference of condition concerns the medium above this substratum. The substratum of a pelagic form is, on the contrary, identical with its medium. Perhaps the solution of the question can be hastened by first determining which two of these modes of existence are the most closely related.

Probably the geobios is more similar in its environmental conditions to the limnobios and halobios, than the latter two are to each other. For in the first place we found while considering the diplobios that this is most frequently a combination of geobios and limnobios, much less frequently of geobios and halobios or of halobios and limnobios. This can mean only that the environmental conditions of the geobios and limnobios are more similar, than either of them is to the halobiotic conditions. The main difference between the land and the freshwater is that in the former the medium is atmospheric air, in the latter water. The atmospheric air always contains some percentage of water, it is sometimes heavily charged with it, and this contained water is usually fresh. So not only in the substratum but also in the kind of water in the medium above it these two environments are alike. On rocky sea coasts, on the beach bared by low tides, the oceanic life meets the terrestrial. Molluscs, Barnacles, Sea Anemones, even various Annelids, Crustacea and Tunicates become daily exposed to the action of the atmosphere, but without ill effects. In similar way the terrestrial and freshwater organisms cope successfully with changing conditions at the

boundary of the freshwater and the land. Land animals can withstand heavy rains, even sometimes prolonged submergence after heavy rains, as I have observed in the case of the Ants of western Texas, and most freshwater animals can withstand considerable evaporation of the water that contains them.

But where freshwater comes in contact with salt the fauna is always notoriously scant, as in the case of marshes, like the Everglades of Florida, that become seasonally overwashed by high tides of the ocean. Species that can live both in fresh and salt water are relatively rare, and have been called by Möbius (1873) euryhaline. So, according to Johnson (1903), there are out of many hundred known species of polychaetous Annelids, an essentially marine group, some twenty-four that are not exclusively marine. Johnson writes: "they belong to only five out of the forty-odd families of the Polychaeta; and of the five, three have each but a single species in fresh or brackish water." Of these twenty-four, 10 (42.5%) are limited to freshwater, 2 (8.3%) are limited to brackish water, 3 (12.5%) can live in both fresh and salt water, 4 (16.6%) in both salt and brackish water, and 5 (20.8%) in all three kinds of water.

It has seemed to me of interest to compare with these Annelids the environmental relations of the Rotatoria. The valid species of this group described up to 1903 are about 469 in number. Of these 335 are restricted to freshwater; 62 exclusively to the sea; 49 occur in both freshwater and the sea; 10 in both freshwater and continental salt basins; 8 in freshwater, the sea and continental salt basins; 5 are restricted to brackish water; and none are restricted to continental salt lakes. So in the Rotatoria 71.42% of the known species are restricted to freshwater, 13.29% to the oceans, 1.96% to brackish water; while the remainder,

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known to withstand change in the constitution of the water, is only 14.23%.

The Polychaeta, accordingly, are mainly marine, and the number of species known to withstand changes in the quality of the water is slightly greater than the number restricted to freshwater; the Rotatoria are mainly freshwater organisms, and the number of their species known to withstand water change is slightly less than the number restricted to the sea. The significance of these data is simply this, that transition from fresh to salt water is not facile. This conclusion is also evidenced by the paucity of life in brackish water, the mixture of fresh and salt that changes frequently in its proportion of salt. The meeting point of fresh and salt water is then a positive barrier to most animals. At every river mouth there is open a road for migration from the sea into the river, and in the reverse direction, but it is fenced off to most organisms by the change in the medium; river and sea have both a far richer fauna than the mixed water at their junction. And on this account it is probable that little of the freshwater has become peopled from the sea, or the sea from the freshwaters.

It results that the littoral life of the sea shows the greatest diversity of animal groups, and at the same time that the limnobios agrees more closely in its environmental conditions with the geobios than with the halobios. In figurative example these three kinds of life may be considered as points on an imaginary angle, placed in such a way that the geobios is closer to the halobios and limnobios than these are to each other.

For the various reasons given, and in the absence of any satisfactory geological basis, it seems to me that Simroth is right in regarding the meeting point of sea and land as the bionomic centre from which most primitive life has origi-

nated. It would seem least likely that the freshwater was the original home, for it has the least varied fauna. The littoral marine fauna, particularly the bottom life near the shore, shows the greatest diversity of groups, and its environment is the meeting point of rain, salt water and atmosphere, with extremely varied climatic conditions. The freshwater would then have become peopled to greatest extent by the path from the sea over the land to the freshwater, and to less extent by direct migration from the sea; this would result from the consideration of the paucity of euryhaline and brackish water forms. If the more general geological view is correct, the surface of the land must have been much moister in early periods than it is at present, much more in the nature of a marsh, so that the terrestrial origin of many freshwater animals need not appear improbable. Thus from the littoral halobios of the shallow water would have originated in one direction the plankton and the abyssal halobios, in the other the geobios and limnobios. The diplobios would have arisen later by a combination of any two of these three; and the entobios may well have been formed independently in all of these environments.

This view seems to my mind more consistent with the data of distribution and environmental influences, than that which regards the pelagic life as the most primitive. We do not mean to imply that all known animal groups have come from the littoral fauna of the sea, far from it, rather that most of the more comprehensive and older groups may have had such an origin. It is quite possible that the land became populated very early, perhaps before the freshwater and before the pelagic life of the sea arose; and that certain of these earliest terrestrial forms have formed descendants that are now marine or freshwater in occurrence; this is a consideration that no one has elaborated more fully and consistently than has Simroth. It may even be that the

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earliest life was terrestrial, in the old times when the land was moist and warm, and that the littoral fauna of the sea came from this source. But however this may be, there is very little reason to believe that the marine plankton is primitive and the pelagic existence the first.

The severity of the struggle for existence upon the land, its complex and rapidly changing environmental conditions, seem to have been responsible for the occurrence of the greatest number of species there, and the occurrence of the most complex and diversified organisms. The processes of extermination must have been most forceful upon the land also, and just this is what accounts for the absence to-day upon the land of simpler and more primitive groups. Thus the present lack of generalized organisms upon the land, and the relatively small number of animal groups, is no good objection to the view that the land may have been the ancestral home of many groups that are now aquatic or wholly extinct.

While on this subject the distribution of the Turbellaria is of significance, a group that is of great importance from many points of view, with undoubted genetic relations to the Annelids and Nemertini, and more problematical kinship to the Ctenophora and Mollusca. One group of them, the Tricladidea, has 317 terrestrial species (according to von Graff, 1896), about 50 freshwater and still fewer marine species. Another group, the Rhabdocoelida, contains only one terrestrial form, and somewhat more than 250 species that are aquatic and of which perhaps the majority are freshwater forms. While the third large group, the Polycladidea, contains about 250 species, all marine and with few exceptions littoral. Taking the Turbellaria as a whole, the most species are marine, but nearly as numerous are the terrestrial forms, while the freshwater ones are the least numerous. The environmental relations

of the Tricladidea in particular would suggest origin upon moist land; or if from other points of view the marine origin would seem more probable, we would have to conclude that the freshwater species have been derived mainly by way of the land and not by direct migration from the sea. There are no freshwater Turbellaria that are pelagic, and very few marine species, so that there is no probability of a pelagic origin of this group. The greater number of the Molluscs are marine, a much smaller number terrestrial, still fewer freshwater forms. The pulmonate Gasteropods in particular include all the terrestrial and most of the limnobiotic species, while but few of them are marine. Like the freshwater Turbellaria the freshwater Gasteropods would seem to have had either a terrestrial origin, or to have been derived from the sea by way of the land. And in the Molluscs the pelagic forms are all highly modified in structure, and not at all primitive.

The analysis of the phenomena of distribution in groups of diversified dispersal can alone decide these questions. Such studies will elucidate at the same time the paths of distribution from the ancestral homes, and all such conclusions will be of great importance in determining racial relationships. It will probably be found that identical conditions of environment have affected different groups in different ways, for in the reaction of an organism to a stimulus the nature of the organism itself plays the greatest part. Caution must be used in drawing inferences from one group to another, on this account. And it should be remembered that the geological basis of interpretation is very insecure and indecisive, and that most of the analysis should be done upon the basis of present conditions of existence. For we shall never know the nature of the earliest life, nor yet the influences affecting it, while we may hope to understand the modern.

D. SEASONAL MIGRATION AND CENTERS OF ORIGIN

There are various habit modes of animals that considered conjointly may throw some light upon questions of the centers of origin of species and more comprehensive groups. One of these is seasonal migration, a change of habitat at particular times of the year. This has been most studied in the case of Birds of passage, where the paths and ranges of migration are most easily determined; to some extent also in Mammals and Fishes. The nudibranch Mollusca of the shallow coastal regions of the sea migrate into deeper water at certain seasons, particularly in search of food; and various pelagic animals have daily and seasonal vertical migrations, which seem influenced by light, temperature and various other conditions. So Parker (1902) ascribes the vertical movements of the Copepod Crustacea to reactions to light. The bionomic group distinguished by us as the diplobios shows also migration, but in a different way, a change of environmental medium at a particular period of the life history. Then one recalls the diplobiotic Amphibia, which live first in water and later upon the land: with few exceptions all of these annually go back to the water to deposit their eggs, and but a small number oviposit upon the land.*

This is, of course, a seasonal migration, and one embodying even a partial change of medium. The Eel is born at considerable depths in the sea, as Grassi (1896) first showed,† then it wanders into freshwater where it lives until it is nearly mature, then swims back to the sea to lay its eggs. The large Salmon of the Pacific migrates up the

* Compare particularly the useful summary of the egg-laying habits of Frogs and Toads given by Miss Sampson (1900), and of the Amphibia in general by Ziegler (1902).

† Eigenmann (1901) has given a good corroborative account of the Eel controversy.

Columbia River to its headwaters, there lays its eggs, and the young swim down to the sea again. These two Fishes are examples of what might be called seasonal diplobiosis, in contrast to that exhibited by the Mosquito where one stage lives entirely in one medium and a later stage in another medium. Seasonal change of medium is shown also in various aquatic beetles (*Hydrophilus*) and Bugs (*Belostoma*) which take long nuptial flights out of the water, then return to it.

What is common in all these phenomena is change of locality or medium at or near the time of the breeding season, a return of the adult to the home (place or medium) in which it was born. There are then two aspects of any migration: the departure from the home and the return to it. The breeding habit is perhaps the central factor in that it stimulates the movement towards the place of birth. And here we may neglect those relatively rare irregular wanderings of some Birds and Mammals that seem to have no connection with the migration proper.

With Birds it is generally held that the Fall migration, the migration in the Northern Hemisphere after the breeding season, is induced by the lack of sufficient food within the breeding area, this lack caused by the oncoming of the Winter's cold. This is a reasonable and probably good explanation, because it is mainly insectivorous species that migrate, whose food becomes reduced by cold weather, and birds of the shores and lakes whose feeding grounds become covered with ice. But the answer to the problem of the cause of the Spring migration, that one towards the old nesting site, is much more difficult to give. Various factors have been assigned to it, such as "physiological unrest at the time of mating," and a "homing instinct." It would be out of place and beyond our subject to discuss all the ornithological views concerning these factors, and

for them reference must be made to the important works of von Middendorff (1855), Palmén (1876) and Gätke (1900), and to the useful reviews of Palmén (1891) and Newton (1899).

The nature of the impulse to return to the home of birth, the seeking of the cradle, is very far from satisfactory solution, and I feel myself incompetent to discuss it. But the actual migration itself, and the production of the young in the old medium or site, may this not throw some light upon questions of ancestral distribution?

The particular question is whether we may or may not regard the geographical area or the medium where the individual undergoes the first portion of its existence as the ancestral home of the species. If affirmatively answered, then a Toad and a Salmon would have been originally freshwater forms, and an Eel halobiotic; and Birds nesting near the Arctic Circle and migrating southward in the Fall would have been boreal in origin. A Sea-turtle oviposits upon the sunny sea beach, it would then have been terrestrial; equally a Mosquito must have been once wholly aquatic! But what is the reason for deciding that in a diplobiotic species, or one that has seasonal geographical changes, the bionomic environment of the young is more ancestral than that of the adult, or the breeding area more primitive than the Winter quarters? We cannot drag in here the help of the recapitulation theory, it is a feeble support and younger stages of the individual are no more ancestral than older ones. Then is there any reason to maintain that the mating habits themselves are more conservative, therefore possibly more primitive, than other habits? At first interrogation one might be inclined to say that this were so, but a comparison of breeding phenomena shows that it is not. All Birds lay eggs, most of them incubate the eggs; but there is enormous variety

with regard to the construction of the nests, the placing of them, and the feeding of the young. Modern Birds make up such a homogeneous assemblage, that one would not expect such differences in the breeding habits were the latter conservative. The anurous Amphibia, the Frogs and Toads, when we disregard the arboreal species, appear remarkably alike in general habits, they are all insectivorous, saltatory, more or less crepuscular or nocturnal, moisture-loving; but how greatly they vary in breeding habits! They may deposit the eggs in water, or at its margin, or surround them with mud; they may not guard the eggs, or the male may nurse them in his pharynx or the female in the skin of her back, or the male may wrap the egg strings around himself and then burrow into the earth. So among Insects the Flies are a homogeneous group; but they may be oviparous or viviparous, lay the eggs upon water or earth or vegetation, in decaying organic matter or even upon living animals.

There is no necessity to mention further cases, for of all the habits in most animals those concerned with breeding, disposition of the eggs and care of the young seem eminently variable. Environments of the young therefore cannot be held to be ancestral, either on the basis of the recapitulation theory or on the view that breeding habits are more conservative than others. Indeed, to regard the surroundings of the young indicative of ancestral environment would lead to some absurd results. It would mean that the ancestor of a Mosquito lived entirely in the water, whereas its modern larva has to come to the surface of the water to breathe, and in all its fundamental structure, the hard cuticula, the tracheae, etc., resembles a terrestrial form. And because a Horse-fly lays its eggs in decaying meat we should have to conclude that its ancestor once lived in meat,—a manifest absurdity.

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Environment of the young, accordingly, cannot be taken as a criterion of ancestral environment in the case of the diplobios. And I can see no good reason why the breeding area of a migratory species, as a Bird, should be considered the original home of its race, even though certain ornithologists maintain such a view. There is much in favor of the idea, first suggested by Wallace if my memory serves me right, that avian migration began at the time of a glacial epoch, which forced Birds away from the Polar regions to the equator, and that Birds moved again towards the Poles following the regression of the ice caps. But the duration of any extensive period of glaciation was surely long enough to allow considerable transmutation of species while they were arrested at the equator, so that immediately ancestral forms would have been equatorial in origin, and not present in the areas where their modern descendants breed. Then there are many cases among Birds where of two closely related species, one is extensively migratory and the other not, as the Song sparrow and the Lincoln's sparrow of North America. In general the question of migration in Birds offers so many perplexities and complexities that extreme caution should be used in determining by it centers of origin of species. And while the ancestors of the anurous Amphibia may have been aquatic, the habit of most of the modern representatives of the group to lay eggs in the water is no proof of this.

When seasonal migrations are more fully understood than they are at present, their factors better analyzed, then such phenomena may be expected to materially lighten questions of ancestral distribution; but it is rather premature to reason from the comparatively little that is known at the present time. The path of a seasonal migration may also not be indicative of a path of racial dispersal. And it might be fairly said that the habit of seasonal migration

would be subject to modification in quite or almost the same degree as any other habit; for it is surely dependent upon other more fundamental habits.

In this chapter we are concerned only with the bearings of environmental distribution upon the settlement of problems of genetic relationships. Centers of origin of species and their paths of dispersion can, however, in most cases not be determined until these genetic relations are first understood. So this particular aspect of environmental distribution is of little help in analyzing phylogeny, though the two should always be conjointly considered. The two are rather mutually explanatory.

Adams (1902) has summed up the criteria of the determination of centers of origin as follows: "1. Location of greatest differentiation of a type. 2. Location of dominance or great abundance of individuals. 3. Location of synthetic or closely related forms (Allen). 4. Location of maximum size of individuals (Ridgway-Allen). 5. Location of greatest productiveness and its relative stability, in crops (Hyde). 7. Location of least dependence upon a restricted habitat. 8. Continuity and directness of individual variations or modifications radiating from the center of origin along the highways of dispersal. 9. Direction indicated by biogeographical affinities. 10. Direction indicated by the annual migration routes, in birds (Palmén)." The fourth of these criteria will not hold for many animals, and we have pointed out that the tenth is of doubtful value. The others may all help in ascertaining centers of origin and lines of dispersal.

How far the distribution of fossils is a sure guide to ancestral distribution and dispersal will depend upon the mode of life of the extinct species, and the liability of their remains being scattered by water currents from their original areas. The decaying carcasses of freshwater and land

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animals may be carried out to sea by rivers, particularly during times of freshets; gases engendered by decomposition lighten the specific gravity, and so aid transportation. This is well known to have been the case in Vertebrates. Walther (1893) has argued very interestingly to explain in a similar way the extensive occurrence of many of the fossil Ammonites. He starts with the facts of the mode of life of the modern *Spirula*, *Argonauta*, and *Nautilus pompilius*, all of which feed mostly upon the sea bottom and only occasionally come to the surface. Then he reasons that the fossil Ammonites probably led much the same existence, were littoral and not pelagic; that at their death the chambered shell, filled with gas, rose to the surface, and by oceanic currents would be driven from the proper habitat of the animal, and ultimately become stranded upon some far distant sea beach, as a gift from the unknown. Just in this way do the shells of the modern *Spirula* become widely dispersed. Therefore the geologic locality of an Ammonite fossil need not have been its home. And we might add, cosmopolitan distribution of fossil Nautiloids and Ammonites would then be no proof of equality of temperature and other bionomic conditions in the earlier seas.

Such phenomena as these we should bear in mind when paleontologists assert, as they do so often and so strenuously, that paleontology alone can decide positively questions of genetic relationships. And sometimes they reason in a circle. They define particular strata and so their relative age by particular fossils, the "Leitfossilien"; then determine the relative age of fossils by the strata in which they occur. As a rule only remains of hard parts are preserved, and then usually only under favorable conditions of enclosure; many groups, those most important to the phylogenetist, have left no trace in the rocks. Even of the

Vertebrates of past times probably not more than one in a million or several million individuals has chanced to leave fossil remains, impressions or casts. For over this continent roamed less than two hundred years ago millions of Bison, but now in many places where they were formerly numerous there may be vestiges of their trails, but frequently not a horn or a bone of them is to be seen on the surface of the ground, or is turned up by the plough. The discoveries of paleontology are exceedingly valuable, but there is no reason to expect the discovery of all connectant races; and as Walther has insisted, the paleontologist should have a knowledge of the bionomics of living groups. Huxley wrote in 1874 that "the ultimate test of the truth of a phylogenetic hypothesis is the historic record of the succession of living forms contained in the fossiliferous rocks"; and Cope (1896) repeatedly insisted that paleontology furnishes the only positive evidence of transmutation. But as a matter of fact, the paleontological record gives very sparse information; and further, the geological succession of fossil-bearing strata is frequently far from being positively determined.

E. ENTOPARASITIC LIFE IN THE ANALYSIS OF DESCENT

The distribution of entoparasites is of very considerable interest, though it has been woefully neglected by students, and therefore it will be worth the while to consider some of its aspects.

The terminal stage of a given entoparasite may occur in several different species of hosts, but more frequently, and this seems to be particularly the case with the Nematodes, is limited to one species of host. Thus it is generally true that a host infected with Nematodes carries one peculiar to itself; and that when a parasite at a particular stage of its existence occurs in different species of hosts,

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only one of the latter is its proper host while the others are accidental ones. An entoparasite restricted in its mature condition to one single host would have to be regarded to be no older, as a species, than that host; for if it were older it might be expected to occur in a number of closely related hosts. That is to say, if a particular entoparasite occurs in only one species of host, it is probably capable of existence in that host alone, and therefore probably has transmuted, changed in its specific characters, at approximately the same rate as the host has. But an entozoan that can and does live in quite different hosts would seem to have more plastic adaptability, and may be genetically older than any one of its hosts; for by virtue of its plasticity in reaction it could remain almost unchanged while its host is undergoing greater transmutation. In this way, from the range of its distribution, one may decide more or less surely of the relative age of a particular parasite. This brings out also the result, that though most entoparasites are racially inferior to their hosts, are members of more primitive groups, in some cases they must be undergoing transmutation when their hosts are, but not at equal rate.

From still another standpoint the character of the terminal hosts helps to explain the racial age of entozoa: entoparasitic forms cannot be older than their terminal hosts, that is in their parasitic condition they cannot be older. In this regard it may be of interest to compare the hosts of the mature stages of the main groups of entoparasites. The Cestodes are limited mainly to Vertebrates, especially Fishes, with a single genus (*Archigetes*) in Annelids. The digenic Trematodes occur also in their adolescent stages mainly in Vertebrates, a single one being found in a Mollusc, another in an Annelid (*Echiurus*), one in a *Myzostoma*, and one in a Siphonophore. Von Graff (1903) has considered

the parasitic Turbellaria collectively: the greater number of species of their group are free, and entoparasites are found only in the sub-groups of the Acoela (one species), and Rhabdocoelida (eighteen species); eight of them occur in Echinoderms, six in Molluscs, two in Crustacea, and one each in *Echiurus* and *Phascolosoma*. The Acanthocephala and Pentastomida at their terminal stages occur only in Vertebrates; the Gordiacea in Insects (accidental hosts excepted); the entoparasitic Nematoda mainly in Vertebrates, but also in Insects, Arachnids, Crustacea, and Molluscs. The Myzostomida are limited to Crinoids and Echinodermata; they are known even on fossil Crinoids.* From their occurrence mainly in Vertebrates, the Trematodes, Cestodes, Acanthocephala, and Pentastomida are groups that in the parasitic condition can be no older than Vertebrates, and from this point of view they may be decidedly more recent than the entoparasitic Nematodes and Turbellaria. This matter should of course be considered in any treatment of the relative racial advancement of these different groups. The hosts of many of the Nematodes are groups of probably earlier origin than the Vertebrates; hence the entoparasites of the latter are probably more recent than the entoparasites of other hosts. Thus the analysis of the hosts can throw some light upon the primitiveness and the plasticity of their parasites, though each case should be interpreted very cautiously. And this does not at all imply that the free ancestors of parasitic Nematodes need be more primitive than the free ancestors of parasitic Trematodes.

In a suggestive paper von Jhering (1902) has drawn attention to the converse position, that distribution of entoparasites helps to explain genetic relationships of their hosts. His argument is that if identical species or genera of para-

*Entoparasitic members of other groups are known, as of the Rotatoria, Mollusca, Crustacea, Insecta, and Anthozoa.

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sites occur in different genera of hosts, that the latter must consequently be of common descent. That is to say, such parasites must have come from a common ancestor, the diverse hosts then also from a host ancestor infected by that parasite ancestor. While this conclusion need not necessarily follow, it has some degree of probability. In this way von Jhering analyzed in particular the occurrence of the *Acanthocephala*. Zschokke (1904) has employed the same reasoning with reference to the distribution of certain Cestodes of the marsupial Mammals. In another place Zschokke (1903) has presented a suggestive interpretation of marine parasites in freshwater Fishes. He shows how migratory Fishes, such as the Salmon, serve to carry entozoa from the sea into the freshwater, and in the reverse direction; and how from the bionomic relations of the parasites the original home of the host may be determined. So in the case of the euryhaline Salmon, we found that the path of its migration alone, and the locality of its breeding grounds, do not indicate its original home; but since the greater number of its entoparasites are known to belong to the marine entobios, then the probability is convincing that its ancestral home was the sea, and not the freshwater where it spawns. It is in fact as Zschokke (1903) writes: "Each parasitic fauna comes to be to some extent a mirror image of the biology of the host, of its habits of life and especially of its relations to those creatures that share the habitat with it. Each change of nourishment and residence of an animal finds its echo in the changes in the helminthic condition."

Entoparasitism is the most extreme case of parasitism, one in which one or more stages live within another creature. In almost all cases there is an initial stage that passes a short free existence, usually aquatic, such a free stage being usually necessary to accomplish the transference to

another host. Where there is change of host there may be more than one such period.

It is generally held that the establishment of a second host has arisen and is promulgated by the habit of a rapacious animal to devour others infected with parasites. And accordingly it has been maintained that to understand the bionomic center of origin of a particular group of entoparasites, possessing change of host, attention should be devoted not to their terminal but to their first hosts. This idea may be correct for some few cases, but should be followed with great caution, because it is not always possible to distinguish between racial first and racial second hosts, certainly not merely from the sequence of hosts in the ontogeny. For in the history of a race of parasites, a species might have become parasitic either in its adult stage or in some earlier stage. There is greater probability that it is the adult stage, because most internal parasites have descended from ectoparasites, and many ectoparasites do not attach themselves to hosts until they are more or less full grown. A parasite might thus have accommodated itself in the adult condition first to a Vertebrate, then later a younger stage of it have adapted itself to a Mollusc or some other form less specialized than a Vertebrate. In such a case the Vertebrate would be the racial first host, though not the first in the course of the ontogeny of the parasite. Here the ontogeny would be a reversal of the phylogeny with regard to sequence of hosts. We have in mind particularly the Trematodes. Most of the ectoparasitic species have as the only host a Vertebrate, usually a Fish; while the entoparasitic (digenic) Trematodes have a change of host, *e. g.*, some live first within a Mollusc and later within a Vertebrate. Because it is practically certain that the digenic Trematodes arose from ectoparasitic forms, more or less like those we know to-day, it would

seem that their primitive host must have been a Vertebrate also, and that the Mollusc was a host acquired later by the Trematode becoming parasitic at an earlier age. This is a more reasonable and simple explanation than to suppose that the Mollusc was the first host, and that the Vertebrate became a second racial host by its habit of eating Molluscs.

To my knowledge no one has given this interpretation of the racial origin of change of host, certainly not for the Trematodes. It can be decided for each group of entoparasites, on the basis of the kind of hosts of the more primitive ectoparasitic species. But not in all groups need the ontogeny of an entoparasite reverse the racial acquisition of its successive hosts. For there are cases enough where members of a certain genus or family of entozoa have mainly aquatic hosts, to such an extent that aquatic hosts should be regarded as the primitive condition; then if an aberrant member of such a group lived in its adult condition in a terrestrial animal as its terminal host, we should have to decide that this kind of host not only appears latest in the ontogeny, but also was the last kind of host acquired by the race. We would then conclude that in some cases of the entobios the host of the adult stage is the first racial host, that of an immature stage the second racial host; and that in other cases the sequence of hosts in the ontogeny would exactly correspond to their sequence in the phylogeny.

Enough has been said to show what a strong right arm environmental distribution may be in the study of descent, though the exposition has not been carried beyond the broader outlines. A comprehensive and thorough treatment of environmental distribution is as yet a desideratum. And in conclusion it may be stated that this subject, habits,

and structure should always be considered conjointly, and that no one of them can be adequately comprehended by itself. Many of the earlier systems of classification in which groups were founded upon the basis of habits cannot stand in the light of more thorough modern criticism; yet one group is an exception, that of Spiders, and this whole group is as definable upon habit characters as upon structural relations. But there was this value in them, that they drew attention to modes of life, phenomena that are being too much disregarded by students in laboratories and museums. It is time that the good old-fashioned word naturalist were reinstated in its full original significance, and that there were fewer biologists, zoologists, botanists, histologists, entomologists, physiologists, and other hermit members of the scientific family. An organism must be interpreted from its many aspects, and not merely from its dead body. For there is a transmutation of habits quite as much as of structure, and the former is probably initiative to the latter.

CHAPTER II

HEREDITY AND EMBRYONIC DIFFERENTIATION

By heredity we understand that process through which one generation comes to be like a preceding one, and by embryonic differentiation the process of change from the egg to the adult condition. These are mighty questions which have long engaged thoughtful minds, for they lie at the very root of all problems of growth and organic change, and knowledge of them must be the very rudder of the phylogenist. Some concept of these processes, some idea based upon the results of the best corroborated empirical work, is a necessary antecedent to any investigation of the phenomena of transmutation, because we can never understand heredity of change until we understand heredity where no racial modification is concerned.

In the brief space of a chapter many considerations must be neglected and no adequate historical treatment of the subject can be given. There has grown up an enormous literature upon these subjects. Able reviews have been given by Delage (1903), Hertwig (1898), Weismann (1902), and Wilson (1900). What I shall have to say is in the main concerning the behavior of the germ cells, a subject upon which much of my own work has been done. What is to follow is a partial exposition of that modern standpoint which seems to me most substantiated by observation and experiment.

A. HEREDITY

There are two modes of studying heredity. One by the examination of the germ cells themselves, which are

the initial stages of every individual cycle; and the other by the study of hybridization (cross-breeding), that is by the analysis of the inheritance in the offspring. The second method enables one to determine the relative amount of inheritance each of the offspring receives from each of the parents, and the general mathematical laws governing such inheritance: it is a statistical study of inheritance, of the sum of the qualities transmitted. So Galton (1897) has given a supposed "law of ancestral inheritance," the accuracy of which has been contested; Mendel (1865) has shown that in the sweet pea parental qualities are transmitted in a particular ratio, some latent, some active; and de Vries (1901) has demonstrated how valuable the results of hybridization are in distinguishing between mutations and variations. This method has also suggested many valuable working theories, helpful in the study of the germ cells. But the study of hybridization, full of promise as it is, can give only a statistical statement of the amount of inheritance; it does not serve to explain the manner of the transmission, but exhibits only the end result. Heredity, that is the process of transmission of the inheritance, can be analyzed only from the study of the living substance concerned in the process of transmission. And so we shall limit ourselves to the germ cells, because it is the process and not the end result in which we are here interested.

In the many-celled animals, the Metazoa, there are various kinds of cells composing the body, but following particularly Weismann* we distinguish two main kinds of them, germ cells and body (somatic) cells. The essential difference between them is in regard to their reproductive

* Throughout reference will be made to Weismann's last, comprehensive work of 1902, which contains his matured conclusions, rather than to his numerous earlier studies. Most of his views go back some fifteen years or more.

ability: the mature body cell is incapable of reproducing a whole individual, but certain of the matured germ cells have this power. For there are two kinds of germ cells, egg cells (ova) and sperm cells (spermatozoa). There is between them not only the long recognized difference of structure and division of labor, the ovum huge, laden with nourishment, usually without the power of locomotion, the spermatozoon minute and motile. But another difference in that only the ovum is reproductive, it alone in the process of cleavage forms the embryonic cell mass; the spermatozoon has no reproductive ability because no power of division which is the only known method of reproduction. Certain ova are able to produce a whole individual without being first fertilized by a spermatozoon, but no spermatozoon by itself can do this. Therefore the egg cell is fully reproductive and so generalized; the spermatozoon is non-reproductive, because excessively specialized, it is the fertilizing cell. Both contribute equally to inheritance, as we shall see, but only the ovum is reproductive.

Protozoa differ from Metazoa in this essential particular, not that they are one-celled or are composed of but few cells, but that they have no distinction of body cells and germ cells. Contrary to the opinion of Weismann this does not imply that a Protozoan is equivalent to a germ cell of a Metazoan. It is rather comparable to both body and germ cell, with the distinction that it does not have these parts disposed in different cells. For there are parts of an Infusorian that do not always persist from generation to generation, but in the event of reproduction by binary fission are formed *de novo* in one of the daughter individuals; such parts are then equivalent to the body cell elements of a Metazoan.

The processes taking place during growth and division of a cell may be determined by a combination of three

methods. One is by the determination of the sequence of change and of the substances most directly concerned, through observation of the sequence of structural phenomena; this is the morphological method. Then there is the microchemical investigation of substance change during the different periods. And the third method is the experimental one, the attempt to gauge the processes by studying reactions when the stimulus is quantitatively known, by isolation of certain cellular portions, by decreasing or increasing operative stimuli, etc. All these methods are of importance, must be carried out conjointly, and the value of each is of course in direct proportion to the amount of its contribution to our knowledge of these processes. So far the first and third have proved most fertile in result. We know little enough of what goes to make the life of the cell, but some points have been gained that seem to give a good foundation to build upon.

In any egg cell the living substance, protoplasm, is in the form of a central body, the nucleus, contained within an outer sheath of cytoplasm. Each of these constituents is demonstrably very complex structurally and chemically. In many cases a third portion is to be distinguished, the centrosomes, minute bodies usually so small as to be visible only during cell division, and usually lying in the cytoplasm. These centrosomes are intimately concerned with protoplasmic movements during cell division, even perhaps are important dynamic regulators of this process; and it would appear to be the general rule that the spermatozoon on entering the egg introduces one or more of them. But there is no evidence that centrosomes are intimately concerned with the process of heredity.

Verworn (1897) has concluded "that neither the nucleus nor the protoplasm [cytoplasm] alone play the chief part in the life of the cell, but that both in equal manner

are concerned in the production of the vital phenomena." That both are concerned there can be no doubt, but it is probable both are not concerned in equal degree and manner. For there is increasing evidence to demonstrate that the nucleus is the center of most constructive growth activity, that it changes food substance into living material, and passes some of the latter over to the cytoplasm, this conclusion dating particularly from the work of Claude Bernard (1878) and Kossel (1891). In rough expression: food is taken up from without the cell by the cytoplasm, transmitted by it in somewhat changed condition to the nucleus, there synthetically elaborated into living material in which state some of it passes out again to the cytoplasm. Numerous experiments have shown that when the nucleus is removed from a cell, the enucleate piece is incapable of growth, but that the fragment containing the nucleus has the power of replacing the part removed.

The question has narrowed, however, within still smaller limits. The nucleus contains a variety of structures or parts differing chemically though each is not a single chemical compound. There is in the period when the cell is not in division, when it is in the "rest stage," a bounding nuclear membrane enclosing the thinly-fluid nuclear sap in which may be freely suspended minute granules known variously as lanthanin, oedematin or oxychromatin globules. Transversing the nuclear sap is a network of linin fibrils, suspended upon the latter viscid globules called chromatin, and caught in meshes of this network the nucleoli, bodies occurring in varying number, position, and form. Without going into further details with regard to the varying composition of the nucleus, there is good evidence to conclude that two particular substances are most intimately involved in the directive regulation of growth, the chromatin and the linin. The chromatin since the investigations

of particularly Flemming (1882) and Kossel (1891) has been fairly well demonstrated to be a combination of substances, one of which is nucleinic acid, which play the leading part in constructive growth; but that the linin must be considered with it we shall try to show.

The chromatin within the nucleus is always locally connected with linin, either placed upon it or enmeshed within it, as I have shown elsewhere (1901a). We can say that all chromatin is in physical association with linin, though all linin may not be so connected with chromatin. During cell division the chromatin and linin cease to compose a network, and form a number of sharply circumscribed bodies, the chromosomes; they become clearly delimited by the chromatin globules moving together into dense and compact masses. The chromosomes are not masses of chromatin alone, as they are too generally considered, but of chromatin enmeshed in or surrounded by linin, as Carnoy (1885), first showed. Because of this intimate connection these substances should always be conjointly considered. The number of these chromosomes is a fixed one for the species, and in far the greater number of cases an even number; the form of them seems to be to some extent dependent upon their number: long, bent, or curled threads when they are few, short rods or spheres when they are numerous. In each successive cell generation of a germ cell the chromosomes reappear in like form and number. From this phenomenon Van Beneden (1883) was the first to conclude that each is a persisting individuality, and not a structure formed anew in each generation. This has received corroboration from so many sides and from so many points of view that the majority of investigators to-day are maintaining it as proven. The evidence to the contrary is all purely negative. This means that the chromosomes are separate bodies, not only during cell division

when their boundaries are well marked, but also during other periods of cellular life. In some cases their boundaries can be optically distinguished even in the rest stage of the cell, when their linin composes a branching network with the chromatin globules loosely distributed along it. And there is good reason to hold that they always remain separate, even though their boundaries cannot always be distinguished.

This idea of the individuality of the chromosomes is a very important basis in the modern concept of the process of heredity, and all positive evidence speaks for the solidarity of its foundation. In cell division each chromosome divides into two equal parts, one part going into one of the daughter cells and one into the other; this division is an automatic splitting of the chromosome along its length, and so far as we can judge by observation it seems to be a mathematical halving. Each daughter cell then receives one half-portion of each of the chromosomes of the mother cell, and so the chromosomes become equally transmitted to the daughter cells. Then each daughter cell usually grows somewhat in size before it divides again, so do all of its chromosomes increase in volume. This is a very short statement of the hard-won results of many observers. We can say that as by division each cell comes from a preceding cell, Virchow's doctrine of "*omnis cellula e cellula*," so each chromosome is derived from a preceding one. In each generation the cell undergoes profound growth changes, possibly even all of its substance becomes chemically changed, else there could be no maintenance of the normal cell size. Similarly each chromosome grows again to the normal size. A chromosome is an individuality persisting from generation to generation quite as much as a cell is, neither is continued unchanged yet neither is a new formation. Whether one prefers to call chromosomes

individuals or cellular organs is a matter of little importance, the point is that they are structures continued from one generation to another.

But we know still more of the behavior of these chromosomes. It is proven that in the act of conjugation of a spermatozoon with an ovum, which is the process known as fertilization, the spermatozoon introduces into the ovum just as many chromosomes and these of the same form and volume as those contained in the ovum. Van Beneden's classic memoir of 1883 first showed this; and first showed also that in the cycle of cell generations, called ovogenesis, leading to the formation of the mature ovum, as in the one leading to the formation of the mature spermatozoon, the spermatogenesis, the last cell generation has only one-half the number of chromosomes present in the earlier generations. Consequently, by the act of fertilization, the normal number, that characteristic of all other generations, becomes restored. Then Henking (1890) and O. Hertwig (1890), as most recently Dublin (1905), have proven that the processes of spermatogenesis and ovogenesis run parallel courses, that there is an essential correspondence between them. There is still considerable conflict of opinion regarding the details of these complex processes, which is very natural since men have worked upon different objects and from very different points of view. The results of my own studies on spermatogenesis (1901*a*, 1901*b*, 1904, 1905) have led me to the following conclusions, which are now receiving confirmation by a number of students, both botanists and zoologists, and most recently by Dublin for ovogenesis also. In these and other papers of mine all the varying opinions have been treated, so that it would be out of place to go over all this ground again. It will be understood that in some points the following account corroborates views of earlier workers, in

others conflicts with them, while one particular conclusion is new, the one relating to the conjugation of paternal with maternal chromosomes.

In spermatogenesis there follow upon one another a series of cell generations called spermatogonia, the exact number of which has not yet been ascertained for any single species of animal. In all of them the chromosomes occur in the full or normal specific number and in each division they are halved longitudinally (equationally); each daughter cell then receives one half-portion of each chromosome of the mother cell. In the spermatogonia the chromosomes are present always in an even number, with the exception of a few cases in Insects which do not concern us at present, and have been treated by me elsewhere. So we find them in the number of four, twelve, twenty, twenty-four, or some other even number; in the greater number of known cases the number is below sixty. A comparative study of the chromosomes in a large number of Insect species showed me that in some cases particular pairs can be recognized, differing from other pairs in size and form. So if there be fourteen chromosomes two are alike in size and form but different from any others, another two larger than any others; so the components of each pair appear alike in size and form, and in these characters differ from the members of any other pair. Even in the case of a Newt, where there are as many as twenty-four chromosomes, there could be demonstrated twelve pairs of graduated volumes and forms. This conclusion reached rapid confirmation at the hands of Sutton (1903).

Now what is the significance of such pairs? As we shall subsequently proceed to show, each spermatozoon, the end of a spermatogenetic cycle, instead of containing *e. g.* twelve pairs as does a spermatogonium, possesses no pairs of like chromosomes, but twelve single, unlike chromo-

somes. The mature ovum, the end of the cycle of ovogenesis, contains also twelve single and unlike chromosomes. Clearly some process must have intervened to displace corresponding chromosomes. The significance of this phenomenon is readily explained in the light of our knowledge of fertilization considered together with the persisting individuality of the chromosomes, otherwise it would be wholly inexplicable. Fertilization is the act of union of a spermatozoon with an ovum whereby each contributes twelve unlike chromosomes, and thereby restores the number twenty-four. Any spermatogonium resulting from the cleavage of such a fertilized egg will then have twenty-four chromosomes. Now because the chromosomes of the spermatozoon are all unlike, at least not paired, and the chromosomes of the ovum are similarly unlike, while any chromosome of a spermatogonium has its duplicate in volume and form, it necessarily follows that each particular chromosome of a spermatozoon must be like in form and volume to one particular chromosome of the ovum. Fertilization then re-establishes the pairs: that is the important phenomenon, and not the one that the normal number becomes restored. Accordingly, of the two like chromosomes which together constitute a pair in any spermatogonium, one must have been derived from a spermatozoon, so be paternal, the other derived from an ovum, so be maternal. And this is the simple and satisfactory interpretation of these pairs. Because such pairs have been demonstrated in a number of cases renders it probable that they are universally present in any early germ cell derived from a fertilized egg; but of course they can be optically distinguished only in those species having chromosomes of demonstrably different volumes and forms. The bearing of this upon the hereditary value of chromosomes will be considered later.

The last generation of spermatogonia gives rise by divi-

sion to the first spermatocytes. Characteristic of the latter is an apposition or conjugation of the chromosomes. This is a conjugation of paternal chromosomes (those derived from the spermatozoon) with maternal ones (those from the ovum). If, for instance, the number of chromosomes in each spermatogonium was twenty-four, these unite to form twelve double chromosomes, or bivalent ones, each composed of one maternal and one paternal in close physical connection. Every two like chromosomes join together in this way, while before they were separated. Then follows the division of the first spermatocytes (first maturation division) which results in removing the elements of each chromosome pair into opposite daughter cells, this being the only known cell division in which whole single chromosomes become separated from one another. Thus are produced the second spermatocytes, each of which has accordingly no chromosome pairs and but half the normal number of chromosomes. Each cell of this generation divides into two, during which process the chromosomes become halved longitudinally (second maturation division), just as in the spermatogonia. Each spermatid, so the spermatozoon that develops from it, has a half of each of the chromosomes present in a second spermatocyte. In most cases all of the spermatids are alike in size, and each becomes a functional spermatozoon without further cell division but by a complex process of metamorphosis. The mature spermatozoon is incapable of further division, and the spermatogenetic cycle is concluded.

In the ovogenesis, the comparable process in the formation of the mature ovum, there is a succession of ovogonia, the last of which give rise to first ovocytes. The latter increase greatly in size, and likewise show a pairing of paternal and maternal elements as Dublin has demonstrated. Each of these cells then divides into two second

ovocytes, whereby whole single chromosomes become distributed to different cells. Of these two cells one is very large, the other (first polar body) minute. Each second ovocyte then divides into two ovoids: the first small polar body into two other polar bodies, the larger ovocyte into a small second polar body and into the ovum proper. Like the spermatid, to which the ovum is genetically comparable, the ovum has one-half the normal number of chromosomes and no chromosome pairs. The ovum undergoes no metamorphosis and is alone capable of reproducing the individual, the polar bodies being rudimentary cells that retain the power of cell division to only very limited extent.

There is thus an essential agreement between the processes of ovogenesis and spermatogenesis, particularly with regard to the behavior of the chromosomes. The main differences between them are these: (1) much greater growth of the first ovocyte as compared with the first spermatocyte; (2) only one of the four cells (ovoids) derived from any first ovocyte being capable of reproduction, whereas all four spermatids may be alike; (3) the ovoid undergoing no metamorphosis comparable to that of the spermatid into the mature spermatozoon.

The spermatozoon carries chromosomes of the male parent, the ovum of the female; when brought together in fertilization the normal number of chromosomes is re-established and also the duplication of each kind of chromosome. Therefore the chromosomes derived from the two parents are alike not only in number but also in form and volume: a chromosome of the one series has its exact counterpart in one of the other series.

All these phenomena make up certainly a remarkable coincidence of results. Certain particular cell structures, the chromosomes, persist through all cell generations in the same number and relative size. Each is as much a persist-

ing individuality as is the cell that contains it. Their substance is a mixture of linin and chromatin; we do not know much of the metabolic nature of the former, but there is good reason to regard the chromatin, at least its nucleic acid constituent, as the most important substance concerned in constructive growth activities. In cell division the chromosomes become halved and distributed to the daughter cells with detailed precision. A spermatozoon has a series of them, in one-half the normal number, every particular one of which is optically the counterpart of one in the series contained in the ovum. There is a temporary conjugation of like paternal and maternal chromosomes at a particular and correspondent stage in each germinal cycle, immediately after which takes place a unique kind of cell division whereby every two like chromosomes become removed into separate cells.

Now some one set of cellular structures and substances must evidently be the controlling ones in the process of heredity. Nägeli (1884) assumed a hypothetical heritable substance that he called idioplasm, which he supposed to form a network within the cell body and connecting bridges with other cells. No substance of such distribution has been demonstrated satisfactorily. Roux (1883) pointed out that the complex process of cell division is established in order to bring about the exact partitioning of the chromatin substance, that is, its equal transmission to the daughter cells. He and Weismann more fully than any others and more consistently have argued that this substance is the bearer of hereditary qualities. That is to say, the substance of the chromosomes is the germ plasm. To-day this is the view of the greater number of those who have personally compared the behavior of this substance, by chemical analysis, experiment, or the study of structural sequence, with the other substances and structures of

the germ cells. This is also my standpoint, with the limiting clause that all substance of the chromosomes must be called germ plasm, linin as well as chromatin, until one is proven to be of greater significance than the other. It would then be more accurate to say: the substance of the chromosomes is the germ plasm, the chromosomes control the process called heredity; heredity is the sequence of chromosomal activity.

O. Hertwig first demonstrated in 1875 that the individual cycle commences by an egg cell being fertilized by a spermatozoon; and since that time abundant proof has accrued that in normal development only one spermatozoon is concerned in fertilization. Then Boveri (1889), removed the nucleus from an egg cell of one species of Sea-urchin, and fertilized the enucleate piece with the spermatozoon of another species; there resulted a larva with paternal characters only. Boveri justly concluded that maternal characters were absent because the egg nucleus was lacking, and accordingly that the sperm nucleus is the bearer of paternal qualities and the egg nucleus of maternal ones. This was one of the earliest of many diverse experiments to show that the seat of the hereditary energies is to be sought in the nucleus. And later by an analysis of results obtained when two or more spermatozoa enter one ovum, with particular regard to the abnormal consequent cell divisions, Boveri reasoned that it is in particular the chromosomes that are to be considered the basis of hereditary energies. Here the experimental study is in entire harmony with the morphological.

And in this germ plasm substance, the mixture of the chromatin and linin, and its bodies, the chromosomes, we deal with structures not on the outer confines of visibility, but with material and masses readily determinable by microscopical means. There is nothing hypothetical about

the occurrence of these structures and anyone who will may see them. They are, to pervert a phrase of Huxley, the physical basis of heredity. So convincing is all evidence that the chromosomes are the center of hereditary activities that we need not hesitate to say: just so much as we know of the behavior of the chromosomes, just so much do we understand of the process of heredity. There is no longer any need of conjuring up a hypothetical hereditary substance, or of endangering our equanimity by pyrotechnic hypotheses concerning it.

It is no more a vain hope that students of the life of the cell will come to recognize that it is more to the chromosomes than to any other cell constituents that attention should be given. It is time that broad comparative studies of them in different species should be made, as well as intensive studies upon a particular species. And it is time, and happily there are a few who recognize it, that the investigation of these bodies should no longer be considered a narrow path of cytological inquiry, but rather the very fundamental basis for the study of development. The phylogenist who would know something of the meaning of the individual, before he proceeds to the race, cannot afford to disregard the advances in our knowledge of the chromosomes. We are not anywhere near the limits of empirical investigation of the germ plasm, and so far have attained only a crude state of knowledge concerning its behavior. One should select a number of closely related species and endeavor to find in their chromosomal relations some reflection of the differences known in the adult individuals.

Of considerable value in this regard are the investigations upon the cell division processes of the Protozoa, particularly those of R. Hertwig, Schaudinn and Bütschli, investigations which may well give the interpretation of the

phylogeny of the processes of fertilization, cell division and maturation, and which are showing the successive racial steps in the elaboration of chromosomes from chromatin granules scattered through the whole cell body.

The structure of a chromosome is demonstrably complex. Each of them is a composite of smaller masses, easily visible when the cell is not in division, and each of the latter shows an architecture of still finer corpuscles, microsomes, that are just on the verge of the visible. Were our optical appliances of study still more perfected it is probable that these minutest globules themselves could be resolved into smaller parts, just as striated muscle fibrils can be resolved into smaller elements with every increase in magnification. We remain on strictly empirical ground so long as we consider only the chromosomes in their entirety, or even their largest component parts. But to postulate successively smaller constituents is to extend the inquiry beyond the limits of the visible.

Perhaps no theory has brought out more ideas and certainly none has been more stimulative to the investigation of the chromosomes than the elaboration of Weismann; but he calls in the help of invisible units. The chemist finds some satisfaction in the idea of an atom, as the physicist in that of a center of movement, and the physiologist in that of an ion. The postulation of ultra-empirical units, which has played such an overwhelming *rôle* in scientific interpretations, is fruitful just so far as it aids research, but is no end in itself. It is only one road toward the prize, and really should not be resorted to until other ways have been shown to be goalless. And now just because the study of the chromosomes is in its infancy, because already so much has been won by the empirical study of them as to assure much more important discoveries in the future, we have no need as yet to resort to hypothetical units.

Certain bodies are practically demonstrated to be the controllers of hereditary activities, and the mass of details already won furnish us with sufficient food for reflection at the present. Nearly every one of us is an admirer of the brilliance of Weismann's determinant theory, that is, of its fundamental concepts if not of its subsidiary hypotheses. But the need of it is past; it did its work in arousing many of the present investigations, so that it lives in the latter. Weismann's ideas constitute an essentially molecular theory, like that of Nägeli and some of his predecessors, and like them also is exceedingly complex in its details. Such complexity is a criterion of all theory in an early stage of science, while theories of a later date usually become less complex. We can say that the more simple an interpretation is, the more lucid it is and probably the more fully explanatory. But however this may be, we are entering upon a period of very fertile research, and so many experiments and observations are now awaiting analysis into simple ideas that we should have neither time nor desire to leave them for the sake of wider speculations.

There is but one point in the Weismannian theory that may be broached here, namely, what portions of the germ plasm are the bearers of particular hereditary qualities, and what parts predetermine adult parts. In departure from the theories of Darwin (1874) and Nägeli (1884), Roux (1883) argued that the smallest visible granules of the chromatin are the bearers of particular qualities. Weismann followed Roux in this, but elaborated the theory to include the invisible complexes of the germ plasm. So Weismann conceived of biophores, the smallest elements capable of life and growth; complexes of biophores, the determinants, each of which would contain all the energies necessary for a particular part of the adult; complexes of determinants, the ids, containing each the hereditary quali-

ties of a whole organism; and complexes of ids, the idants, bodies with the hereditary qualities of more than one individual. Weismann identifies the ids with the smallest visible particles of the chromatin, idants with any larger and visibly more complex bodies. He argues that an id would be comparable to a chromosome in the event that the latter is very small, but that a large chromosome would be composed of many ids, so be an idant. To Weismann accordingly a chromosome is the bearer of the hereditary qualities of a whole individual, or even of the qualities of many individuals.

It has come out recently that this idea of the valence of a chromosome is erroneous, and that in most cases a chromosome contains the qualities not of a whole individual or of many such, but only of parts of it. For the chromosomes of a spermatozoon are proven to contain all the hereditary qualities of the father, those of the ovum all those of the mother. The fertilized egg, formed by the conjugation of the two, therefore contains the qualities of two whole individuals, just as Weismann himself has argued. We know only one case where the fertilized egg holds just two chromosomes, namely, *Ascaris megalocephala univalens*; one of these belongs to the egg, the other is introduced by the spermatozoon. In all other known cases the fertilized egg has at least four chromosomes, in the greater number of cases numbers ranging from about twelve to sixty. If we take a case where a fertilized egg has twenty-four chromosomes, this egg before fertilization must have twelve, the sum total of the energies of these twelve would then be equivalent to those of the single chromosome in the unfertilized egg of *Ascaris megalocephala univalens*. As the single chromosome of the latter contains all the energies necessary to the formation of one individual, each of the several chromosomes of the other case should contain then

the hereditary qualities of only a portion of a whole individual.

The following observations confirm this conclusion. In a number of objects, in most where the chromosomes are not very small or numerous, the chromosomes can be shown to be of different sizes and forms. This phenomenon was referred to earlier, and it was shown that in the germ cells before the first maturation division the chromosomes are paired in volume and form, and that of each pair one component was derived from an ovum and one from a spermatozoon. In other words, in such generations of germ cells there are two series of chromosomes, one paternal and one maternal, and each paternal one has its visibly exact counterpart in one of the maternal series. Every two corresponding ones conjugate in the synapsis stage, this being then a conjugation in each case of a paternal with a maternal one; and in the following cell division every two like ones become transported into separate cells, so that every ovum, as every spermatozoon, comes to have only one series of chromosomes, and these all unlike. Then after confirming these observations and conclusions of mine, Sutton (1903) offered a suggestive, simple, and probably correct explanation of the sorting of like chromosomes into different cells. He argued that the *raison d'être* of this first maturation division, which is so different from all other cell divisions, must be just to effect the separation of like chromosomes. And he reasoned that every two chromosomes that are alike in volume, visibly alike, probably have equivalent hereditary energies; hence that their complete separation prevents duplication of like hereditary qualities in the spermatozoon or unfertilized ovum. And then Sutton showed this to be best interpreted to mean that each chromosome is the bearer of one set of qualities, and not of all the qualities of a whole individual. And surely

chromosomes that differ in form and volume cannot be regarded as equivalent in value. Then Boveri (1902, 1904), in the lucid logic so peculiar to him, concluded from an analysis of the behavior of chromosomes when eggs are fertilized by more than one spermatozoon: "that not a fixed number but a fixed combination of chromosomes is necessary for normal development, and this means nothing else than that the single chromosomes must possess different qualities."

So, contrary to Weismann, the view is fairly well founded that each chromosome is the bearer, not of the qualities of a whole individual, but of a single quality or of a set of particular qualities. This is a very important empirical conclusion, for it makes it possible by morphological and physiological observation to trace back particular adult qualities to particular chromosomes, and so opens up possibilities that until very recently seemed incapable of test.

Accordingly, the substance concerned most intimately in the process of heredity, the germ plasm, is the substance composing the chromosomes, and the different chromosomes of any cell have probably different qualities. We know something already about these chromosomes, they lend themselves readily to microscopical investigation, and continued study of them promises much more. Just so far then as we understand the behavior of the chromosomes, just so far can we interpret heredity. There is no need for the mental construction of hypothetical elements, the study of heredity is now settled upon an observational basis.

In 1882 Flemming wrote: "If, in order to take only one important example, the protoplasm of the egg cell were nothing more than a morphologically homogeneous mass with yolk granules scattered through it, or even a fluid, as it has been called with all earnestness in recent time, we would be obliged to leave to chemistry all answer that the

egg brings of the conditions of development. But has this substance of the egg a structure, can the latter and the composition of the threads in particular regions of the cell body be different, then can be sought therein a basis of developmental predestination in which the one egg differs from another; and this search will be possible with the microscope—just how far no one can say, but its aim is nothing less than a true morphology of heredity.” Fleming adds “that to-day it must appear impossible or inconceivable that such a condition can be realized by optical means.” But that is exactly what we are realizing at this day. The wonderful complexity of the germ cells is being made known, and we are proving that one generation of beings is like another because it has similar chromosomes.

B. EMBRYONIC DIFFERENTIATION

The stages passed through from the egg cell stage to maturity, the differentiation of the embryo into the adult, sets problems that must always be considered conjointly with the question of the nature of heredity; the two together constitute the phenomena called growth. From the wide embrace of the relations these become the most fundamental and most complex of all questions concerning life.

In order to understand modern standpoints it is necessary to go back somewhat into their origin. The fullest historical treatment is that of Delage (1903), and mainly from his exposition is given the condensed account of some of the earlier views presented in the next two paragraphs.

The oldest document on these subjects is the *Manava-Dharma-Sastra* of the Hindoos, which says that only the father contributes to the formation of the embryo, the mother giving but the mould for its development. This view continued with modifications in the school of the Spermatists, reaching its height with the discovery of the

spermatozoa by Hartsoeker, a pupil of Leuwenhoek, at the end of the Seventeenth Century; Hartsoeker supposed that within the spermatozoon was an organism complete in all its parts like the adult—the homunculus of his corroborators. This is the first expression of the preformation of the adult in the germ, a preformation in the spermatozoon, the female furnishing simply a place and nourishment for its growth.

In opposition arose the Ovists, particularly under the leadership of Harvey's (1651) classical (and the first) treatise on embryology, a work which one may read to-day with great profit and with regret that few of the moderns are capable of such clear expression. He maintained that the uterus produces the egg, and that the spermatozoon fertilizes the mother and by a sort of "contagion" renders her capable of producing eggs. The Ovists held then that the egg alone furnishes the embryo, that the spermatozoon furnishes nothing but an impulse to the formation of eggs. This school included many famous as pioneers in biological thought, such as Swammerdam, Malpighi, Haller, Bonnet and Spallanzani. They, too, held that the adult is preformed in the germ, but contrary to the Spermatists maintained that the egg is the germ and that the mother plays the important part in generation. Bonnet said in 1776: "The germ placed from the commencement in the egg receives from the fluid which the male furnishes the principle of a new life. That starts it to develope and frees it of the narrow bounds which hold it." This preformation theory supposed the egg to contain an embryo like the adult in all its parts but a miniature of it; an embryo that has simply to unfold and increase in size to become exactly like the parent. This was the hypothetical process to which the word evolution was first applied. It postulated that within this germ was another like it but in still smaller miniature,

within this still another, so that each germ would have in successive encasement germs sufficient for all following generations. The Spermatists argued for the same kind of successive encasement in the case of the spermatozoa. Even up into the Nineteenth Century such ideas of preformation continued.

It was Wolff (1759) who gave in his lucid and masterful doctor's thesis, based upon careful observations, the death-blow to the old preformation doctrine. He showed that all the parts of the adult are not preformed in the germ, but that the embryo proceeds by a series of steps or acquisitions, organ appearing after organ, so not by preformation but by epigenesis.

Yet a third view has held sway, the one that the father produces some organs of the embryo, the mother others. This idea appeared early with the Greeks in the Sixth Century B. C., and was adopted by Empedocles, Hippocrates, Aristotle, Athanasius, Avicenna, Linnaeus and Buffon; their only empirical basis was the one of the apparently intermediate character of some hybrids.

To-day we know that the spermatozoon is incapable of generation by itself, but that in fertilization it contributes hereditary qualities equally with the egg. We know also that the egg is frequently capable of complete generation without fertilization, as in cases of parthenogenesis, but also that no animal can reproduce through an indefinite number of generations without an act of fertilization. We can say, accordingly, that in these matters the Ovists were more nearly right than the Spermatists. It is also known that the essential of fertilization is the conjugation of an egg cell with a spermatozoon, and not the influence of the latter upon the maternal body; yet the seminal fluid has some action in certain cases upon the body of the mother, as in those insufficiently understood conditions that zoolo-

gists know as "prepotent influence," and botanists as "xenia." But over and beyond all these we do know that the egg and the spermatozoon do not contain completely formed organisms, and that embryonic development is not simply a process of unfolding of perfected but miniature parts. In other words, the growth changes of the embryo constitute differentiation, a becoming-different, and not a mere increase in mass.

But what is the nature of this differentiation?

In the first place the germ cells are not simple but exceedingly complex structurally and chemically; so far as can be determined by observation this is a high degree of complexity, and bettered microscopical appliances do not show any underlying homogeneity, but this complexity extends beyond the horizon of visibility. Indeed, the heterogeneity becomes more and more manifest the further we penetrate by observation. Therefore, contrary to Spencer, development of the individual is not a progress from the homogeneous to the heterogeneous, for the starting-point itself is heterogeneous.

In the second place a particular kind of egg always develops into a particular species of adult. Side by side, floating in the same sea water in identical conditions of light, temperature and pressure, develop an egg of a Sea-urchin and one of a Tunicate; the first always becomes a Sea-urchin, the second always a Tunicate. There can be but one meaning to this: that the species is as much marked in the egg as in the adult, though not by the same characters. That implies there must be as many different kinds of eggs as there are of adults; and that if the differences between the eggs are distinguished with greater difficulty, it is because egg differences are less readily perceptible, and not because eggs are more alike than adults are. For each egg, to become a particular species of adult, must have peculiar

growth qualities: it must have the qualities of a particular species. Yet growth qualities have a determinate physical and chemical basis, they cannot exist apart from what we call structure and substance; therefore each particular species of egg must have its own peculiar structures and substances. This is the only permissible conclusion from the definite developmental differences of egg cells.

Obviously, then, the adult, though not in all its parts preformed in the egg, must be to some extent predetermined by the nature of the egg. How far is embryonic differentiation a series of added steps, epigenesis, how far the gradual differentiation of a plan already predetermined in the egg? This is the question in its present clothing.

The complexity of the egg is demonstrated beyond question. Most recent study brings out not only this, but also the fact that these different structures and substances have a precisely regular and definite distribution in the egg cell. This has been shown very conclusively by Whitman (1878), Roux (1895), Boveri (1901), Conklin (1902, 1905), Wilson (1903, 1904), and Fischel (1897), to mention only a few of the more prominent investigators. Boveri showed that the egg of one Sea-urchin, before its first cleavage, has particularly colored substances distributed in a regular manner, and that each of them goes to form a particular part of the adult. Conklin has proved this more thoroughly and exhaustively than any one in his memoir (1905) on the development of Ascidians, describing in detail the precise arrangement of certain substances, the rapid rearrangement of them that can be seen when the spermatozoon enters, their accurate sorting out to become each a particular definite organ of the adult. Wilson and others reached much the same conclusions from the analysis of developing fragments of eggs. There is nothing haphazard in this process; all sequence is in perfect order, be-

ginning with the precise localization of different substances in different regions of the egg, an arrangement that itself is probably initiated in the germ cells of generations antecedent to the mature ovum. This is the most recent acquisition to our knowledge of growth and differentiation, yet perhaps the one most securely founded upon observation. It is a very precise localization of different organ-forming substances, though they are in regulated movement as particularly Conklin has shown. Therefore Roux was correct in his theory of the egg as a composite of substances with diverse growth energies, a mosaic-work; and to some extent correct in regarding the cleavage of the egg as a process that imposes boundaries, in the form of cell walls, to these substances, just so far correct as he takes account of the movements of the different substances before and during cleavage.

And thoroughly corroborative is all the analysis of the process of cleavage, egg division, of different animals. These studies upon the exact position, origin and fate of each of the cleavage cells, the study known as cell-lineage, started by Whitman (1878) and Vejdovský (1888), and carried out by a host of later workers, are showing that all cleavage is determinate, to use the term of Conklin (1897): that is, precisely regular, each cell determined to rise at a particular time, in a particular place, and to form a definite part of a particular later organ. No morphological investigations have been pursued with greater accuracy than these, and they have shown that each egg so studied has a perfectly determinate mode of cleavage, with no element of chance, but perfect order and sequence in all details.

There is but one justified conclusion from the great series of facts so briefly referred to, particularly the initial complexity of the egg with the precise localization and movement of all its substances, and the orderly succession

in the cleavage process. That is, that the formation of the adult, or what is called embryonic differentiation, is determined by the energies of the particular substances of the egg. So much can be said with a fair degree of certainty. It is equally true that particular parts of the adult are prelocalized in particular egg substances. There is then predetermination and prelocalization; these phenomena admit of no other interpretation.

Yet, to take a special instance, it will be said that an adult bird has a horny beak, and that horn substance as well as a beak are absent in the egg. But this does not conflict with our idea of predetermination. This beak is prelocalized in the egg in the form of a particular substance, though that substance is not horn; by perfectly gradual change that egg substance becomes horn substance and a definite beak, the continuity in the change being gradual. This is a gradual differentiation of a continuous growing substance; it is epigenesis in that in one stage it differs from the condition in a preceding stage, but not epigenesis as this word was originally defined, not an interrupted succession of steps. It would be best to use for it the term predetermination, or, even better, differentiation, which implies a gradual becoming-different. The point is that this differentiation is a gradual proceeding from definite substances of fixed disposition.

There have been experiments performed by Driesch (1892b), Morgan (1895), Wilson and others which have been interpreted as contradictory to the idea of predetermination or prelocalization of adult parts. One of these is the taking of a Sea-urchin egg when it is in a cleavage stage and so consists of several cells, and shaking these cells apart. To take an instance of one in an 8-cell stage: when the eight cells are artificially separated, each of the eight is said to produce a complete or perfect larva but of

one-eighth the normal volume. Driesch then argued that in the early stages at least all parts of the egg are equipotential, each capable of producing any part or the whole of the adult. That is of course a perfectly logical conclusion. But he and others have gone further than that and reasoned that therefore there can be neither predetermination nor prelocalization, but that the process of the embryology is strictly epigenetic. Different writers have urged different objections to this second conclusion, which is really a *non sequitur*.

So some eggs are known, as that of the Ctenophore, where an isolated cleavage cell does not always form a perfect larva or adult, but only a portion of it. Then it is not yet proven that dwarf larvae formed from isolated cleavage cells of Sea-urchins are quite normal in structure. But the most decided objection has been clearly stated by Conklin (1905), that of the evidence of orderly complexity and movement of egg substances: "These observations have taught us more with regard to the actual differentiations of this egg [Sea-urchin], as contrasted with the potencies of its parts, than all the experiments which have ever been made. . . . It seems rather that the true explanation of this discrepancy is the one originally suggested by Roux (1892, 1895b), *viz.*, that there is a difference in the regenerative or regulative capacity of different ova and that in the experimental studies referred to we are dealing with indirect development or regeneration, as contrasted with direct or normal development. . . . If this view of the relative independence of differentiation and regulation be correct the conflict between the results of cell-lineage and of experimental embryology disappears, for the prospective tendency or the actual differentiation of a blastomere and its prospective potency deal with two distinct things." And this appears to be an entirely logical position to take.

In the development of all eggs, not molested or injured by experiment, all the observational evidence is for predetermination and prelocalization; there is not a particle of proof of equality of the different regions or substances of the egg. Egg fragments secured by experiment may develop into partial or into whole embryos; when they develop into whole embryos the occurrence of predetermination and prelocalization is not by any means disproved, but simply there is demonstrated their power of regeneration or regulation. When an adult Planarian is cut transversely into two, and each of the halves regenerate the part removed from it, this does not prove that the one part is like the other; no more does an experiment which isolates cleavage cells. The nature of this process of replacement of a part lost by accident does not concern us here, it is quite a different question that has bearings upon what is known as plasticity of organisms; what interests us here is the analysis of normal development when the processes have not been interfered with.

Predetermination seems so accordant with the phenomena that the idea of epigenesis appears quite unsatisfactory and baseless. Development does not commence with the homogeneous or equipotential, but with the heterogeneous and heteropotential; differentiation is visibly gradual and continuous, not a series of disconnected steps. The catch-phrase of Driesch (1893) that "the prospective value of a blastomere is a function of its position," is found to be erroneous by recent studies, and to have no more value than as a statement of an idea that is passing. Strict epigenesis is unthinkable, almost as thoroughly disproven as is strict preformation; yet the old preformation concept was nearer to the truth. The idea of predetermination, the successor of the last, is incompatible with epigenesis, and attempts to harmonize the two, as notably that of O. Hert-

wig (1898), appear self-contradictory. The egg has either an initial complexity and order, or it has not; if it has, that initial structure with its involved set energies must dominate and control differentiation; if it has not, the egg can have no such control, and purely extrinsic factors must constitute the agent.

Our present evidence of predetermination and prelocalization is mainly for the egg cell. If it is true for this it should be true also of the spermatozoon. Since in the process of fertilization some portion of the spermatozoon, as usually some of its flagellum, is generally left outside of the egg, so that only a portion aids in the formation of the embryo, its predetermination of parts has no such great interest. But the whole head of the spermatozoon always enters the egg, the portion containing the chromosomes, so probably also always its middle piece (which usually contains a centrosome), and sometimes the whole spermatozoon enters. For this reason it would be desirable to pay some attention to the exact arrangement of substances within the spermatozoon, of substances that are to be compared with those in the egg. The substances and structures of the spermatozoon have long been known to be very complex and of particular distribution, and in some objects all of these have been traced back continuously to certain substances in the earlier generations of the sperm cells.

But the egg is the reproductive element, it forms the cleavage cells, it is the arena of differentiation, so in it rightly have the phenomena of differentiation been sought. What egg substances are most controlling in development? Specific egg substances are most clearly distinguished in the cytoplasm, less perceptible on the whole are substance differences within the nucleus. Now because the nuclear chromosomes seem to be the controlling agents in growth

and heredity, it would follow that they and their component substances may be the centers of differentiation. Chromosomal behavior might be the basis on which we are to interpret embryonic development. Differentiation may be the outcome of those hereditary energies which comprise the activities of the chromosomes; and we cannot separate the question of how one generation becomes like another from the question of how the egg becomes an adult.

This idea of nuclear control of both heredity and differentiation we owe in the first instance to Roux (1883), who from the start has maintained a consistent position in the matter and is now finding most men turning to his views. He argued primarily from the standpoint that all indirect cell division is a means developed for the purpose of the exact distribution of the substance of the chromosomes. Then he and Weismann reasoned that there might be qualitative distribution of this hereditary material, that in the cleavage of the egg some cells would receive certain parts of it, other cells other parts, and thus differentiation be due to a sorting out of germ plasma of different qualities to different regions of the embryo. Each of Weismann's hypothetical determinants by qualitative chromosomal divisions would be distributed to particular cells, and by the growth energies inherent in them determine the further development of these cells. The egg would be the only cell capable of reproducing the whole, because it alone contains all kinds of determinants. A standard objection to Weismann's view is regeneration in an adult of a missing part by a part unlike that restored; to circumnavigate this difficulty Weismann argues that each cell, besides receiving definite determinants that control its growth, receives others also that are held in reserve and remain inactive until a missing part is to be restored. This subsidiary

hypothesis is of course a very weak point in his argument, and rather contradictory to the whole genius of the reasoning.

Another view is that of de Vries (1889), that the nucleus controls differentiation by emitting particles, pangenes, into the cytoplasm, which there guide the process of differentiation. Conklin (1902, 1905) has shown how the nucleus regularly distributes fluid substances into the cytoplasm, at each cell division when the nuclear membrane dissolves away, and he maintains that many cytoplasmic substances may so come from the nucleus, and thereby determine cytoplasmic modification. One of his most surprising discoveries is that all the substance that forms the ectoblastic germ layer of the embryo comes probably from the nucleus of the egg cell. Driesch has argued that ferments are contained in the nucleus, and pass out of it into the cytoplasm where they set going particular chemical energies.

So most of the numerous views concerning nuclear control of differentiation group themselves round two sets of explanations: (1) qualitative transmission of the substance of the chromosomes from nucleus to nucleus during cell division; and (2) migration of this or other substances from the nucleus into the cell body at certain definite periods. There is not necessarily any conflict between these two mechanical explanations, and they might even be associated. But it is worthy of remark that emigration of nuclear substances has been demonstrated, and in particular of chromosomal constituents (linin and oxychromatin), while qualitative chromosomal divisions have never been observed. This speaks for the greater probability of the standpoint of de Vries and Conklin.

Boveri (1887) showed for the cleavage of the egg of *Ascaris megalocephala* that in the division of cells destined

to be body cells large portions of each chromosome become thrown out into the cytoplasm. Then Goldschmidt (1904) followed the later history of these discarded chromosomal pieces; he showed that they remain alive and active within the cytoplasm of the body cells, and reasoned logically that they may determine the growth energies of the cells that contain them. Goldschmidt goes further, and brings a considerable mass of evidence to show that distinct substances within the cytoplasm of various cells in other animals also are to be directly compared with such substances as these. And then he starts a suggestive theory. Lubosch (1902) distinguished in the egg cells two kinds of chromatin: idiochromatin, the seat of hereditary activities, and trophochromatin, that concerned with general metabolism. Then R. Hertwig (1902) observed in Protozoa the emigration of chromatin into the cytoplasm where it forms living networks, that he called chromidia. Goldschmidt now reasons that every animal cell is essentially binuclear: "It contains a somatic and a propagatory nucleus. The first represents the somatic functions, metabolism and locomotion. . . . The propagatory nucleus contains particularly the hereditary substance, to which comes also the power to produce a new metabolic nucleus. The two kinds of nuclei are usually combined in one nucleus, the amphinucleus. The separation may follow in greater or lesser degree; a complete separation is rare, most usual a separation into a mainly propagatory, but still mixed nucleus, the cell nucleus in the usual sense, and the chief mass of the somatic nucleus, the chromodial apparatus." *

The possibility of the complete substantiation of Goldschmidt's theory shows how many modified views, and ones

* Schaudinn, (1895) was the first to conclude a primitive binuclearity, on the basis of his observations on *Amoeba binucleata*.

full of promise, fertile minds may yet bring into the analysis of well-known phenomena. Whether qualitative chromosomal division is a factor in differentiation we do not know; but there is at present considerable evidence that the passage of chromosomal constituents from the nucleus into the cell body may be an important agency in embryonic differentiation.

So we come to see how the analysis of the behavior of the chromosomes opens a wide field, not by speculative but by empirical methods, for determining the nature of both heredity and differentiation. This view is at least the simplest and most consistent.

We will leave the discussion of these great problems at this point. There is yet no theory of heredity and differentiation that is fully explanatory, and speculation should not too rapidly outrun the slower interpretation from observation and experiment; the tortoise may yet outstrip the hare. The aim of this chapter has been to show that the problems are more fully upon an observational basis than ever before, that they are no longer purely speculative and subject to the loose rein of any imagination. By careful analysis of observations upon certain portions of the processes the wider interpretation of the whole is to be reached. There is ample scope for the creative imagination in dealing with the perceptible, before we have to reason from the imperceptible. Every interpretation that points out coincidence in seemingly diverse phenomena is an approximation towards broader understanding, and just such interpretations are of the most lasting value. Heredity cannot be explained by the mathematical study of inheritance alone, rather the latter can only then be correctly interpreted when we understand the nature and the behavior of the germ plasm.

CHAPTER III

RELATIONS OF MODES OF REPRODUCTION AND CONJUGATION

PHYLOGENISTS have in general too much neglected the important phenomena of reproduction, and have too frequently tried to classify and relate the different kinds of reproduction from preconceived ideas of relations of groups, rather than taking the reverse course; the botanists, however, have sinned less in this respect than the zoologists. This is not very surprising since until within the last thirty years or so but little was known of the more fundamental details of these processes. Reproductive relations must be considered as an important basis in analyzing racial descent, for it is perfectly obvious that all transmutation is dependent upon reproduction, as are also the phenomena of heredity.

And here more fully than in any other field of inquiry it is necessary to commence with the simplest organisms, with an interpretation of the processes as they are found in the Protista. Students of these lower forms have begun to recognize the importance of the knowledge of modes of reproduction, to the extent of using them in determining relationships of groups. The origin of the processes in the Metazoa and Metaphyta, where they are more uniform, is to be interpreted by the nature of them in the Protozoa and Protophyta. Of immediate interest to the phylogenist are questions such as the following: the significance of alternation of generations; the relative primitiveness of sexually and asexually produced individuals, and of hermaphroditic and dioecious ones; and the possi-

bility of the determination of the degree of specialization on the basis of differences in modes of reproduction. Back of all these questions is the fundamental one of the genetic relations of nucleus and cytoplasm of the cell, a problem broached by Bütschli (1876, and later papers), Calkins (1898b) and others, which is of importance because of its broad bearings in regard to the substance most intimately concerned in heredity.

A. REPRODUCTION AND CONJUGATION

It is a possibility that life first arose by spontaneous generation, autogeny, from non-living bodies. Such a formation has never been seen, however, despite the reiterated precocious promises of physiologists to artificially produce living protoplasm, and our empirical knowledge is only of the formation of life from preceding life. Reproduction is always a form of division; and any normal process of the formation of new individuals from preceding ones is known as reproduction. Regeneration is essentially different from reproduction, when it is used in its strict sense to imply the new growth (Darwin) of parts that are lost (whether normally or by accident). While the latter is frequently associated with asexual reproduction, it is nevertheless a distinct process.

In the Protozoa the following kinds of reproduction are known:

(1) Binary fission. When the individual reproduces itself by division into two parts that are exactly or approximately equivalent in size and structure. This occurs among the Foraminifera apparently only in one-chambered and naked forms (*e. g.*, *Hyalopus*). It is not general in the Radiolaria, but is found in most Sarcodina and is the usual mode in Flagellata and Ciliata.

(2) Budding. When the parent individual cuts off in-

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dividuals much smaller than itself. This is the prevalent process in the Suctoria, and occurs also in the Radiolaria, Heliozoa, certain peritrichous Ciliata, *Noctiluca*, and certain Myxosporidia.

(3) Fragmentation (sporulation, conitomy). When the nucleus of the parent individual divides into many nuclei, by successive binary divisions or by simultaneous multiple division, the cytoplasm not dividing until this process is completed, then the cytoplasm divides into as many portions as there are nuclei, and each small portion of cytoplasm with a contained nucleus is set free as a motile individual or spore. Usually the whole parent animal divides into spores; when it does not, the non-fragmented portion is incapable of long continued life, and seems to consist to large extent of katabolic waste products. This is the exclusive mode of reproduction in the Sporozoa, the most general one in the Foraminifera and Radiolaria, it occurs also in the Heliozoa and certain Sarcodina lobosa (*Trichosphaerium*, *Arcella*, *Diffugia*, *Amoeba*, *Paramoeba*).*

These modes of reproduction intergrade in manifold ways, too numerous to be described here; and in any of them the nuclear divisions may be direct or indirect (simple or complex). Because we are endeavoring to decide which of these modes is the most primitive in order to reach on this basis a decision as to the relationships of the groups exhibiting them, it is clear that we should not have in mind any previous conceptions as to the relationships of the different Protozoa. There is much reason to hold that differences in reproductive phenomena should offer important foundations in deciding racial descent.

Kinds of reproduction that recur in very different organ-

* Our knowledge of these processes in the Protozoa is due largely to the studies of Bütschli, Richard Hertwig, and particularly Schaudinn, though a large number of others have contributed their share. An excellent recent summary has been given by Lang (1901).

isms, that are more general, would seem probably more ancestral than kinds of limited occurrence. Thus budding would appear less likely an ancestral process than either of the remaining two, because its relative infrequency militates against its being very ancient in origin. Then it is very rarely the exclusive mode in any species. The general view is therefore probably correct, that either binary fission or fragmentation is the primitive process. Depending upon the decision between the last two would be the answer of the question, *e. g.*, whether the Flagellata or the Sarcodina should be considered the more primitive forms. That is to say, were the most primitive Protozoa free-swimming and monaxonic, provided with flagella, or were they of more irregular form, without flagella and moving by pseudopodia or protoplasmic flowing? Now the products of binary fission are like the parent; those of fragmentation are motile and usually minute spores, provided either with pseudopodia (pseudopodiospores) or with flagella (flagellospores, zoospores), and different from the parent.* But fission into two equal parts, with preformation of organs before the daughter individuals separate, implies a greater perfection of process than a breaking of the individual into many pieces, each of very simple structure and obliged to pass through a process of differentiation to resemble the parent form. It is particularly this phenomenon of greater simplicity of the offspring, and its subsequent differentiation, that points to reproduction by fragmentation being a more primitive process than binary fission. This is of course only a probability, for many other considerations should be taken into account.

* It is apparent why the spores are motile since they are essentially for the distribution of the individuals of the species. The physiological and morphological distinction between a pseudopodium and a flagellum is very slight, because it is well known that one may rapidly change into the other.

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The general view is that binary fission is the most primitive kind of reproduction in the Protozoa, but the position just taken would seem to have greater probability, and it goes to substantiate the view of Schaudinn that the Sarcodina, and specially the Foraminifera, are more primitive than the Flagellata. We shall never know how the earliest organisms propagated themselves, except that it must have been by division, but there is no good reason to hold that it was by division into two equal parts, much less with preformation of organs before separation of the parts. Fragmentation is the simpler process, and perhaps that form of it the most simple, first described by Schaudinn (1895) for *Calcituba*, where the nucleus breaks at once into many pieces. It would seem to be later specialization that led to production by complex cell division of two regularly equal parts. Further, the nuclear changes in fragmentation are as a rule of less complex kind than in binary fission.

Quite distinct from reproduction in the Protozoa is conjugation of two individuals, as pointed out notably by Bütschli (1876), Weismann (1891), and R. Hertwig (1898). The following modes of conjugation are known for Protozoa, and they are probably genetically related in the order given:

(1) Connections of two or more individuals of the same species without fusion of the cytoplasm or nuclei. This leads to the formation of colonies or states.

(2) Temporary or permanent junctions of two or more individuals of the same species, with fusion of the cytoplasm but not of the nuclei. This is commonly known as plastogamy.

(3) Temporary or permanent conjunctions of two individuals of the same species, with fusion, intermixture or interchange of both cytoplasm and nuclei. This is called karyogamy.

Conjugation processes have not yet been observed for all groups of the Protozoa, but it is probable they will eventually be found in them all. Karyogamy is temporary (transitory) in *Monocystis*, *Noctiluca*, and most Ciliata, but a permanent fusion in the other cases where it occurs; perhaps permanent karyogamy may be the more primitive condition, since it is characteristic of Protozoa supposed from other points of view to be the most primitive. In karyogamy two modes are generally distinguished, according to whether the conjugating spores are alike in size and appearance (isospores), or are dissimilar in these characters (anisospores). The first mode, isogamy or homogamy, occurs in Heliozoa, *Trichosphaerium*, *Protomyxa*, Thekamoebae, *Hyalopus*, Radiolaria, *Podophrya*, and Haemosporidia. The second, anisogamy or heterogamy, in Vorticellidae, Coccidia, Haemosporidia, Radiolaria, and certain Flagellates.

The conclusion that conjugation is in its origin and significance a process distinct from reproduction, admits of little doubt. For reproduction is the formation of new individuals by division, conjugation a reduction in their number by coalescence. Further it is known that both processes may concur in time, or they may be separated by long time intervals, or reproduction may precede conjugation. Again, plastogamy is the genetical forerunner of karyogamy because it is simpler, and with our knowledge that plastogamy has no immediate connection with reproduction it becomes still more evident that karyogamy itself had originally also no such association. The physiological significance of conjugation has not yet been satisfactorily interpreted, but there are certain good reasons to adjudge it to be connected with states of nourishment.

In the Metazoa the only single cells capable of reproducing the whole individual are the egg cells, and neither

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the spermatozoa nor the body cells have this power by themselves. In the Metazoa there are only two kinds of reproduction:

(1) Sexual reproduction, where the new individual commences as a matured egg cell. The egg cell in most cases conjugates with a spermatozoon before reproduction (*i. e.*, its division or cleavage). Thus the egg cell is comparable to a protozoan macrogamete, and the spermatozoon to a protozoan microgamete. But since in the Protozoa there is no close association of reproduction and conjugation, we could not speak of sexual reproduction in them.

(2) Asexual or non-sexual reproduction, where the new individual does not begin as an egg cell, but as an abstraction from the parental body (budding) or by a division of this body into more or less equal parts (fission). There are many good reasons for considering asexual reproduction to be not primitive but secondary in the Metazoa. It differs essentially from sexual reproduction in that the beginning of the new or daughter individual is in the form of a mass of body (somatic or tissue) cells, though germ cells may be enclosed within them.*

Conjugation of germ cells is so general in the Metazoa that it is probably occurrent in all species, though there are still some forms where it has never been observed. In a generation when it occurs the reproduction has been called amphigony (Haeckel), and where it does not, monogeny. In the Metazoa, unlike the Protozoa, karyogamic conjugation is always associated with reproduction, in that it immediately precedes this process. Nevertheless it is not essential to sexual reproduction, for in cases of partheno-

* Perhaps in all cases products of asexual generation contain germ cells. If this were so, it might then be the case that the incapacity of any part of the body of an animal to reproduce asexually, or even to regenerate, would be due to the absence of germ cells in it,—but this is merely a suggestion.

genesis it does not precede reproduction. Balfour (1885) was the first to show that parthenogenesis, development by an unfertilized egg cell, is sexual and not asexual reproduction, and all more recent analyses confirm his opinion. We can state that parthenogenesis is sexual reproduction not accompanied by conjugation, because species possessing parthenogenesis have dissimilar germ cells, and the generation is always by the ovum. But it is probable that in the Metazoa the association of conjugation with sexual generation is the primitive condition, and that parthenogenesis is a secondary modification in which the act of conjugation has dropped out; an able argument on this subject is given by Weismann (1902). In the Protozoa, however, the concurrence of conjugation with reproduction is not primitive. A teleological value of conjugation or fertilization in the Metazoa may be what Weismann (1891) has called *amphimixis*, that is, the mixing of the germ plasms of two individuals with thereby increased opportunities for variation; whether this act serves also to rejuvenate the ovum, on the theory of Maupas (1889), is more problematical.

This conjugation or fertilization of the Metazoa is always of the type of karyogamy. But while the cytoplasm, sometimes not all of it, of the spermatozoon merges with that of the ovum, the nuclear chromosomes appear never to fuse together, but simply to pair together temporarily at a much later stage and generation of the germ cells, namely in the synapsis stage of the first ovocytes and first spermatocytes. This conjugation of the chromosomes was interpreted by me (1901b) to be the last and most important step in the process of fertilization, and its significance was mentioned in the chapter on "Heredity." Plastogamy in Metazoa never occurs between egg cells and sperm cells, such associations being always karyogamic; but cases of it are found in the temporary unions into pairs or bundles of spermatozoa

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within the same testis, more rarely in colonies formed by associations of previously separated individuals (certain Rotatoria, as *Megalotrocha*, and some Corals). Many cases of intimate symbiosis of individuals are probably examples of plastogamy. But in the Metazoa plastogamy is never associated with reproduction.

B. SEXUALITY

And this brings us up to the meaning of the phenomenon known as sexuality. Reproduction and conjugation (fertilization) were shown to be in origin two distinct processes, that only secondarily may come to be associated. Sexuality of individuals exists only in association with conjugation; where there is no conjugation of reproductive elements there is no condition of sexuality, no sex-difference of these individuals.

As generally understood, sexuality is held to imply the co-existence of complemental and dimorphic conjugating individuals, and so we understand it. But that condition is probably the more primitive where the conjugating individuals (gametes or persons) are alike; though the only reason for this view is that similarity would precede dissimilarity, because simpler. Sexuality would not exist, accordingly, in cases of conjugation of similar gametes. Yet it may be remarked that gametes may not be perceptibly different, and yet be actually dissimilar, *e. g.*, differ not in determinable structural characters but in chemical. From this point of view some spores called isospores would really be heterospores, and so sexuality extend back beyond observable limits. Thus sex difference may be an exceedingly old condition even among the simplest forms of life; and indeed it may well be as old as the process of conjugation itself, because the conjugation of two gametes (spores) would appear to be induced by their difference, and at least

conjugation is too precise a process to have originated as a matter of chance. When we use the term isogamy, accordingly, for the conjugation of supposedly similar spores in the Protozoa, we should mean by it only that no perceptible differences are known between the spores, and not that such differences are lacking entirely. Sexuality is then essentially the condition of difference obtaining between conjugating individuals. In the Protozoa these are known as macrospores (macrogametes) and microspores (microgametes), and in this group the former is a female individual and the latter a male. In the Metazoa these two kinds of gametes find their equivalents in the ova and spermatozoa, known respectively as female and male germ cells; the multicellular bearer of ova is a "female," and that of spermatozoa, a "male," in the general sense of the words.

Because conjugation is a process distinct from reproduction, sexuality, being intimately associated with conjugation, has no primary connection with reproduction. There can be no doubt of this conclusion, which is abundantly evidenced by the phenomena known for the Protozoa.

The genesis of sexuality has been this, that out of a state where all individuals were equally capable of reproduction a condition of division of labor has ensued, inducing morphological and chemical differences, between individuals capable of reproduction and conjugation and other individuals capable of conjugation alone. This holds true in the Metazoa both for the germ cells and for the persons, and the male is characterized by his power to conjugate or fertilize, the female by her power to reproduce. A microgamete in the Protozoa, or a spermatozoon or male person in the Metazoa, is an individual that has lost the power of reproduction in becoming specialized for the act of conjugation.

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Sexuality is then the state of occurrence of dissimilar conjugating individuals, and the essential point in this dissimilarity is that only one kind of these individuals has the power to reproduce. This simple interpretation was entirely overlooked by Geddes and Thomson in their theory of "The Evolution of Sex." They endeavored to show that the radical difference between spermatozoon and ovum, and male and female multicellular individual, is that the growth processes of the former are katabolic (destructive), and those of the latter anabolic (constructive), stating the contrast in terms of nutritive growth energies. To be sure the ovum grows to a greater size than the spermatozoon, else it would not be an ovum. But as Ryder (1890) has argued, sex differences cannot be adequately expressed in this brief formula. Indeed anabolism and katabolism are never dissociated, but always concomitant, though the one may preponderate. The formula of Geddes and Thomson neither agrees with the facts nor does it express the essential differences between the sex cells or the sex persons; the theory of these writers is a misstatement and not an explanation. And Ryder himself (1890) is certainly mistaken in assuming the spermatozoon to be the simpler germ cell, and to be the reminiscence of an early flagellate ancestor; for, on the contrary, it is much more specialized structurally and physiologically than the ovum, even to the extent of having lost the power of reproduction.

Our conclusion, that in the Metazoa the ovum is essentially the reproductive individual and the spermatozoon the fertilizing one, expresses the true difference between these germ cells. This difference is reflected even in the sexuality of the multicellular individuals that carry the germ cells. It was argued at some length by me elsewhere (1904*b*) that the male organism throughout the Invertebrates generally, and in the lower Vertebrates also, is cer-

tainly the morphological and physiological inferior of the female. When the sexes are perceptibly dissimilar the male is not as advanced as the female in point of size (which implies duration or intensity of growth) or in complexity of the reproductive organs. Not infrequently the male is clearly more embryonic than the female, as in most Rotatoria, *Bonellia*, and some other forms; while the female is very rarely the more embryonic. And even in cases of hermaphroditism, which are usually protandric, *i. e.*, with a male condition preceding the hermaphroditic, the male state occurs at the stage of lower physical perfection. Only in comparatively trivial characters of secondary sexual structures may the male be the more advanced. In the Birds and Mammals this relation is to some extent reversed, but there too the female reproductive organs are more modified from the embryological standpoint.

However we may regard the relative degree of specialization in Birds and Mammals, there can be no question that the female is the more developed organism in the greater number of animals. There can also be little doubt that in most cases the female is superior in psychical powers, for while in some groups the male terminates his existence after impregnating the female, the latter lives on to carry out the complex activities for the care of the offspring. This difference is best expressed by the statement that the male is generally more embryonic, often as the result of a shorter growth period. These conclusions are not at all in accord with the views of Geddes and Thomson, that the male is more katabolic; rather he is simply less advanced. In the economy of the species the male is frequently of far less importance than the female, so much so, that in numerous cases there are successive generations of females before males appear, while it is impossible that there could be generations produced by males alone. To the phylogenist

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these considerations are important in showing that because the female is the more advanced individual, she should on that account receive greater attention; the female exhibits more fully than the male, in most Metazoan groups, the extent of transmutation of the species. The female is the generatrix, and therefore is far more of a parent than the male who has not the power to reproduce.

C. SEXUAL DIMORPHISM AND HERMAPHRODITISM

There is to be noted in certain Metazoa dimorphism of spermatozoa and of ova. A list of such cases can be found in the papers of Cuénot (1899), Beard (1902), and Lenhossek (1903). Thus in *Dinophilus*, Rotatoria, and Aphids there occur two sizes of ova: from the larger developed female individuals, from the smaller, male. Dimorphic spermatozoa have long been known in prosobranchiate Mollusca, where they were first described by von Siebold (1837). Here there are "worm-shaped" larger spermatozoa, and "hair-shaped" smaller ones. The latest worker on these spermatozoa, Meves (1902), shows that it is not proven that the "worm-shaped" spermatozoa conjugate with ova, and holds that their use is still problematical. The same author also described two kinds of spermatozoa in a butterfly, *Pygaera*. In another Insect, *Euschistus variolarius*, two kinds of spermatozoa had been described by me; in this species the testis is composed of six long chambers, seemingly alike in structure, in a particular two of which the spermatozoa are different from those in the other chambers; these two kinds of spermatozoa of *Euschistus* seem to be different structurally simply in the amount of their cytoplasm; the process of their formation is the same, so that in this respect they differ from the dimorphic spermatozoa of the Molluscs. The only other known cases of dimorphic spermatozoa are those which differ in regard

to the possession of certain modified chromosomes, the heterochromosomes; a critical review of all these cases is given in my last paper (1905). Dimorphic ova and spermatozoa may be found to be of more general occurrence than is supposed. But while both kinds of ova in such cases are capable of reproduction, there is no proof that both sorts of spermatozoa are able to fertilize. Thus the significance of the dimorphism in the latter is not at all understood, though Beard (1902) and Castle (1903) have speculated upon it.

Spermatozoa are male gametes, the individual that carries them is *propter hoc* a male, and because ova are female gametes their bearer is a female. Each fertilized egg cell contains, however, in equal number chromosomes of its own and chromosomes added to it by the spermatozoon, and therefore it, and the whole individual which arises from it by cleavage, contains in equal amounts hereditary substance from the two parents. Sexuality is clearly then not a condition of difference in hereditary potentiality. Sexuality finds its expression and origin in extra-chromosomal differences. When, accordingly, certain writers speak of male and female spermatozoa, and male and female ova, as does Castle, they contradict in terms the general idea of sexuality. For the sex of a germ cell is not a function of its potentialities of inheritance, or future determination of sex, but the expression of its difference in present structure and energies from the cell complementary to it.

When in Metazoa the spermatozoa are carried by certain individuals, the ova by others, that condition is named dioecious or gonochoristic, and we say there are separate sexes. Sexuality of the multicellular individual is therefore a function of the kind of germ cells borne by it. But when both kinds of germ cells are carried by the same individual the condition is termed monoecious or hermaphro-

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ditic, and we say correctly that the sexes are united in one. A hermaphroditic animal is not one without sex, as is so often loosely imagined, not asexual, but one with double sex.

Is the dioecious or the hermaphroditic condition the more primitive? In the Protozoa every zygote (conjugant) formed by the concurrence of two dissimilar gametes (spores) is a hermaphrodite, because it arises as the fusion of two sexes. This is, however, hermaphroditism based on the mode of origin of the individual, or what we will call for brevity "initial hermaphroditism." A Protozoan is not a hermaphrodite in the sense that it is the bearer of male and female gametes, a state which may be termed "eventual hermaphroditism." For in the case of a Protozoan forming gametes by fragmentation it does not become the bearer of gametes but rather loses its entity in their production: therefore a Protozoan is never an eventual hermaphrodite. In the cases where it forms gametes by budding, as in the Suctoria, it produces gametes of only one kind (microgametes), so in this case also is not an eventual hermaphrodite. A Protozoan individual formed by conjugation of dissimilar gametes is then an initial hermaphrodite, but never an eventual one in the sense of being the bearer or producer of dissimilar gametes. And because conjugation of like spores, isogamy, is probably more primitive than conjugation of dissimilar spores, heterogamy; and because there is no sexuality unless the conjugating individuals are unlike; it follows that in the Protozoa hermaphroditism is not primitive, and that when it occurs it is of the initial kind only.

In the Metazoa every fertilized egg cell is a hermaphrodite, because the conjoint of a male and female germ cell; every Metazoan so formed is then an initial hermaphrodite. In point of view of the kind of germ cells arising

in the multicellular body to which this fertilized egg gives rise the individual may be dioecious (when it contains only one kind of germ cells), or hermaphroditic (when it contains both kinds). That is, the individual in such a case is always initially hermaphroditic, but not always eventually. A Metazoan individual developing from an unfertilized egg is initially of course of but one sex, namely female, though, paradoxical as it may seem, it may eventually become a male; no Metazoa arising from unfertilized eggs are known to be eventually hermaphroditic; therefore any Metazoan coming from an unfertilized egg is from the beginning and with respect to its ultimate fate unisexual and never hermaphroditic. When writers in general speak of hermaphroditism in Metazoa they mean not the condition of the fertilized egg, but that of the adult organization. Yet it is necessary to distinguish what has often been confused; initial hermaphroditism, determined by the conjugation of germ cells of different sexes; and eventual hermaphroditism, conditioned by the presence of two kinds of germ cells within the adult body.

Now the great majority of zoologists seem to consider eventual hermaphroditism a more primitive state in the Metazoa than separation of the sexes. Few have maintained the opposite position, but among them are Fritz Müller (1885), Delage (1884), Beard (1884), Pelseneer (1894), and I (1895); Wheeler (1896) grants the possibility of it, though he does not decide for it. It was originally maintained by me that the condition of separated sexes is the primitive one, because in apparently all known cases of eventual hermaphroditism the sexual conditions are not simultaneous so much as successive or overlapping; and I reasoned that when two successive states of sexuality are present in the same individual, the second has become imposed upon the first. For there appears to

be no Metazoan known in which the male and female germ cells develop simultaneously. It is the general rule that in a hermaphrodite the male products ripen earlier than the female, which is known as the protandric condition; here the individual is functionally first male, then hermaphrodite, then female. Very rarely does proterogyny, the reverse condition, occur, though it has been described for *Salpa*, certain pulmonate Gasteropods and some Corals; here the individual is first female, then hermaphrodite. In these cases the individual is then, judging by the times of ripening of the genital products, first unisexual, then bisexual, then finally unisexual again. In most instances these sexual conditions overlap and this overlapping constitutes the hermaphroditic state. But there is one exception to the last conclusion. In *Myzostoma pulvinar*, according to Wheeler's account, the individual is first male, then female, without a true hermaphroditic period; this is the most extreme case of dissociated states of sexuality in a hermaphrodite.

Unfortunately we have little precise knowledge of the origin and history of the sex cells in hermaphrodites, and even what is perhaps the most exhaustive memoir on this subject, that of Ancel (1903), leaves much unexplained. The great difficulty lies in distinguishing male and female germ cells in their earliest generations. We do not know from observation, for instance, for an eventual hermaphrodite, whether the germ cells are from the start sexually indifferent or whether they are potentially and actually dissimilar, though the latter alternative is the more probable.

The writers who suppose eventual hermaphroditism to be the primitive state in the Metazoa give as their main reason the fact that among normally dioecious species hermaphroditic individuals sometimes occur, and argue that this is to be explained as a reversion to an ancestral condition. This is not a particularly necessary conclusion, however; and

ideas of reversion or atavism are elastically turned about to suit the meaning of their users, as are Biblical phrases. From this they reason that the ancestral forms were hermaphroditic, and that this condition of sexuality has become suppressed in certain groups by the suppression of one of the sexes: a male individual would be one that had lost female characters, and a female one that had lost male characters. There is little weight in this argument. The initial hermaphroditism of the fertilized egg has nothing to do with the question, for it is of entirely different nature from the eventual hermaphroditism. No Protozoa have eventual hermaphroditism, so that this condition must have arisen first among the Metazoa. In most hermaphrodites the functional male condition precedes the functional female, in accord with the male being more embryonic than the female and the male germ cells maturing more rapidly. Therefore even in hermaphrodites sequence rather than concomitancy of sexual states is the more usual, and because of its more general occurrence would seem to be more primitive. If eventual hermaphroditism were an earlier condition we could not so well understand this sequence.

There is just as much and even more reason to consider hermaphroditism as a secondary condition that has arisen independently in different animal groups, and the condition of single sex is morphologically and physiologically certainly simpler than double sex. The simplest and therefore probably the primitive sexual condition would be separation of the sexes, each multicellular individual producing only one kind of germ cells.

CHAPTER IV

LIFE CYCLES AND POLYMORPHISM OF INDIVIDUALS

IN no case is the offspring exactly like its parent, for even in binary fission or budding the daughter individual differs from the parents at least in size. The series of changes passed through by an organism in becoming mature, becoming like the parent that formed it, constitute its ontogenetic or embryonic cycle. This cycle may be completed within the lifetime of one individual, in which case it may be called simple; or it may extend over more than one, and then be a complex of two or more simple cycles. The interpretation of life cycles is of immediate value to the phylogenist in its bearing upon the origin and relations of the different known modes of individual development, the connection of these with modes of reproduction, and the determination of the beginning and end of the life history.

Etymologically a cycle signifies a circle, a movement without beginning or end. The metaphysical naturalists of some three centuries ago posed and debated the academic question: does the hen produce the egg, or the egg the hen? Even then, accordingly, it seemed apparent that every organic cycle must have its commencement and its termination. That this is true there can be no question, for such a cycle is the expression of the growth changes of an individual, and living beings because they find an end, which man calls death, must necessarily have also a beginning, else there could be no temporal sequence of individuals.

In the following discussion we shall treat first of the phenomena in the Metazoa, where they are better understood, and then of the conditions in the Protozoa.

A. INTRODUCTORY CONSIDERATIONS

In the first place, two frequently associated but not necessarily interdependent phenomena must be kept distinct, the one being the sequence of kinds of reproduction, and the other the succession of kinds of individuals within the species. This becomes obvious when we approach the intricate and perplexing problems known as alternation of generations and polymorphism of individuals.

As Steenstrup (1842) defined alternation of generations he included alternation of different kinds of reproduction, sexual and asexual, as well as alternation of different kinds of individuals. And most thinkers upon the subject share this view as stated by Claus (1885): "The essence of this consists in the circumstance, that the sexual individuals produce offspring which remain through life different from their parents, but are nevertheless capable of reproduction and as 'nurses' produce asexually a brood, which either reverts to the organization and mode of life of the sexual individual, or again generates asexually and first in its offspring leads back to the sexual individuals." But alternation of sexual and asexual generation, and alternation of individuals differing structurally, are clearly not the same thing, for the former is a condition of division, and the latter a condition of structure. And there may be alternation of modes of reproduction, yet the individuals of all generations be anatomically alike, and no alternation of modes of reproduction, yet alternation as well as concurrence of dissimilar individuals. For this reason it becomes necessary to split Steenstrup's complex idea of alternation of generations into its two parts, and to take these up in succession.

It will be recalled that in the Metazoa there are two kinds of generation: sexual, through egg cells, whereby the ovum

may be fertilized (amphigony) or not (parthenogenesis); and asexual, by budding and fission on the part of the body (somatic) tissues. These correspond to the two kinds of cells, germ cells and body cells, and consequently we have to distinguish in ontogeny between germinal and somatic cell generations. While the two usually accompany each other, *i. e.*, take place in one and the same individual, they are always to greater or less extent independent.

The germinal cycles were considered in the chapter on Heredity. It will be recalled that the mature ovum is the end of the cycle of ovogenesis, and the mature spermatozoon the termination of the cycle of spermatogenesis. The ovum is the more generalized cell with power of reproducing the whole individual, while the spermatozoon is exceedingly specialized and without any such power. The animal in which the point of divergence of the germinal and somatic cycles has been traced back farthest is *Ascaris megalocephala*, where Boveri (1887) first showed that at the 2-cell stage of cleavage one cell is exclusively somatic and the other mixed somatic and germinal, on the basis of a peculiarity in chromosome distribution called "chromosome diminution." This mixed cell at its next division gives rise to a somatic and a mixed cell; this process continues so through five cell divisions in all, at the end of which are found cells that are purely somatic and others that are purely germinal. Cleavage of the egg results therefore in a separation of the somatic from the germinal substance; but clearly only a portion of the somatic substance becomes removed from the egg cells, else the ovum of the next generation could not contain somatic potentialities. The essential peculiarity of the ovum is thus not exclusion of somatic constituents, but preservation of these together with the ability to reproduce the individual.

In asexual generation the commencement of a cycle cor-

responds to the first perceptible beginning of the bud or daughter piece. But in sexual generation the starting-point is always the mature ovum. As notably Weismann has shown, there is a continuation from individual to individual of only the germ cells, not of the body cells, and we can imagine this continuity of the germ cells of the race as an unbroken line and the body cell masses of the individuals composing the race as disassociated points upon this line. It might then be considered as sufficient to demarcate the limits of each individual cycle, in order to determine the first commencement of each multicellular state. But that would be an inadequate statement because not giving expression to the continuity of the germ cells, which are equally essential to the race. The beginning and end of the cycle of the person must accordingly be interpreted from the cycle of the germ cells, from the germinal cycle.

In the germinal cycles the initial stages are easily determined. The spermatozoon, since it has no power of reproduction by itself, is clearly the last stage in its cycle. It is also the most specialized stage. The ovum, which corresponds to the spermatid rather than to the spermatozoon, is the last stage of its cycle, both by analogy with the spermatid as well as by the fact that it is the most modified stage, the one with the greatest amount of deutoplasm (yolk) and with the reduced number of chromosomes. The starting point of the multicellular individual is then the mature ovum, whether it be fertilized by a spermatozoon or not. Therefore the initial stage of the multicellular body coincides with the terminal stage of the germinal cycle. Since either male or female multicellular individuals may arise from an ovum that has not been fertilized, it becomes evident that both the germinal cycles, spermatogenesis as well as oogenesis, of the new generation have their beginning in the cleaving ovum. Accordingly, the

mature ovum is the commencement of the somatic cycle, and the earliest generation of ovogonia and spermatogonia the commencement of the germinal cycles known respectively as ovogenesis and spermatogenesis. The germinal cycle is a progression towards greater differentiation, leading towards that unique phenomenon known as the conjugation of the chromosomes, a process not paralleled in any somatic cells.

Thus it comes that the egg produces the hen, and not the hen the egg.

These considerations furnish the key for unlocking some of the problems of what constitutes the beginning of any somatic cycle. The latter are to be interpreted from germinal cycles, and not the reverse. The commencement of any ontogenetic cycle, whether it be simple or complex, is the mature ovum. Therefore, any individual which reproduces by the agency of ova is the end of the ontogenetic cycle, whether that cycle consist of one individual or of more than one. And now we may proceed to found this view on further considerations.

Somatic ontogenetic cycles may be variously classified according to the point of view that one wishes to express. So according to number of individuals composing the cycle, according to the sequence or kinds of modes of reproduction or of relations of amphigony and parthenogenesis, or according to kinds of metamorphosis in the embryonic differentiation. The following appears to me the most fully expressive of all these relations :

Continuous.	{ 1. Orthoplastic (direct).	
	{ 2. Metaplastic.	
	{ 3. Metagenetic	} Larval
Discontinuous.	{ 4. Heterogenetic	
	{ 5. Ekdytic	} Alternation of generations.

These we will now take up with regard to their mutual relations.

B. CONTINUOUS LIFE CYCLES

By a continuous ontogenetic cycle we mean that condition in which every structure or part that appears at any time of the somatic differentiation passes wholly over into a later structure; in other words, in which no part is formed that does not become moulded over or changed into a later part. In this kind of development there is no part thrown off, and no part that serves only a temporary use without aiding in forming a later part. A structure of one stage is a step in the progression toward a subsequent structure, and never itself an end of development. There is progressive change in which all the nascent structures have their share, and no one of them breaks the general continuity.

Continuous cycles are always completed within the life of one individual, and so are without alternation of generations; they are continuous just because they include no somatic disassociations either of individuals or of parts of individuals. They are also always associated with more or less strictly monobiotic existence, that is, life passed in all its stages under approximately the same environmental conditions and with approximately the same persisting habits. Further, only sexual reproduction is associated with continuous cycles and never asexual. These are a number of characteristics that mark continuous development as a simpler mode than discontinuous, and thereby tend to demonstrate it to be the earlier or more primitive condition. Yet it must be recalled that in some cases continuous development has eventuated as a secondary modification of the discontinuous. Notwithstanding this, however, the relative simplicity of the characteristics of continuous development show it to be the primitive mode of ontogeny in the Metazoa,

and render it very probable that all discontinuous development has arisen as a modification of it.

Two kinds of continuous ontogenetic cycles may be distinguished, as orthoplasia and metaplasia respectively, terms introduced by Woltereck (1904). Orthoplasia is the equivalent of what has more generally been called direct development. By it is meant the condition where each successive stage is an immediate further approximation towards the adult, and where the development may be said to be in a straight line. It implies that all the stages pass the same kind of existence and under the same conditions of environment. By reason of its greater simplicity it is to be regarded as genetically antecedent to metaplasia, which is continuous development where the course of the ontogeny is not at all points a further direct approximation towards the adult stage, but is more or less indirect and may be imagined as a curved or angular line. The latter is development with a free larva, but without discontinuity of structure or process, and good examples of it are the ontogenies of certain marine Molluscs. It is probable that metaplastic cycles are much more frequent than orthoplastic, for the reason that many animal species with continuous development do not pass exactly monobiotic existence, but in their earlier stages live under conditions more or less different from their later. So in the earliest cleavage and gastrulation stages most forms are less locomotory than in later stages, which implies then some slight degree of metaplasia, minute in degree though it may be, rather than exact direct development. For it is a change of environmental states that induces change of habit, and thereby also change of structure and process.

Dissogony is the term applied by Chun (1880) to a condition in certain Ctenophores, as *Eucharis*, where the larva reproduces sexually, then metamorphoses metaplastically into the adult, and the latter also is sexually reproductive.

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The only other known case of disassociation of sexual periods in one and the same individual is *Myzostoma pulvinar*, as described by Wheeler (1896) and by him compared with the condition in the Ctenophores; here it accompanies orthoplastic development, and is a case of successive hermaphroditism where there happens to be a break between the functional male and the functional female condition.

C. METAGENESIS

By discontinuous development we signify, on the other hand, development where there occur breaks in the ontogeny, be they lapses in continuity between successive individuals composing a cycle, or breaks in the nature of larval or foetal organs that do not take part in the formation of later structures. This kind of cycle includes most examples of larval development, all except those mentioned above, and all cases of foetal and heterogenetic development, as we shall proceed to show. It is always associated with marked amphibiosis, or difference in mode of life at different stages.

We may follow Haeckel (1866) in his original definition of metagenesis as "essentially characterized and distinguished from all other kinds of development, in that the generative cycle does not consist of a single physiological individual or biont, but is composed of two or more bionts." Its correct criterion is just this, and not polymorphism of individuals. But we may add to this definition, as is generally done, the idea of alternation of sexual and asexual generations, for this is what distinguishes metagenesis proper from heterogenesis.

Metagenesis must have originated from continuous development, as must have the other modes of discontinuous development. An analysis of the cases of metagenesis shows this to have probably taken place by a lengthening of the embryonic cycle in association with, and probably by reason

of, diversity of mode of life at different stages. Such lengthening of the life cycle presents the possibility, not given by direct continuous development, for successive reproductive periods, therefore for extension of the cycle over more than one individual. And because the different stages may pass quite different kinds of existence, and therefore be in structure and behavior quite diverse, there is opportunity for a succession of different kinds of reproduction. The earlier a larval stage appears in the ontogeny, a stage widely divergent from later ones in its environment and habits, the less likely, *ceteris paribus*, that such a stage would reproduce sexually, because its germ cells would not have had time to become mature. Consequently the reproduction by such stage is generally asexual, and thus has arisen an alternation of asexual and sexual generation, or metagenesis in the strict sense. Continuous development shows one reproductive period, and that sexual; metagenesis a sequence of asexual and sexual.

We previously saw that in the Metazoa sexual reproduction is more primitive than asexual. This was reasoned from the probably universal recurrence of the former in all species, and the only occasional occurrence of the latter. And if a species shows only one of these modes it is always the sexual. Asexual reproduction appears in most cases to take place before maturity of the germ cells. This is evidenced in metagenetic Sponges, Hydromedusae and Scyphomedusae. The only good exception to this rule seems to be the internal buds (statoblasts) produced by the Bryozoa ectoprocta after the sexual products, but in this group also the external buds, those that do not persist through the Winter, may be produced before sexual maturity. All such facts speak for a general condition of association of asexual reproduction with immaturity of the organism, that is, a stage preceding sexual maturity. From

this point of view asexual generation is not a process added after sexual generation, but before it: it is a process interpolated between the initial stage, the ovum, and the end stage of the individual. This view is most accordant with the phenomena so far as they are known. Its importance is evident, for it suggests that in cases of true metagenesis individuals that reproduce asexually are not terminal stages of a metagenetic cycle, but stages interpolated. Of several individuals composing a metagenetic life cycle, that one which generates sexually is the end of the cycle, and the others, even if separated individuals, are not terminal stages. This thought is simply an extension of the idea of the germinal cycle applied to the individual or series of individuals that make up the somatic cycle: in this sequence the decisive criterion is furnished by the germinal cycle, since sexual development is the primitive and original mode in Metazoa. The stage of the ovum marks the commencement of the new cycle. The beginning of a metagenetic cycle is the ovum, the individual immediately arising from it is the first, and the individual that finally produces ova again, the last, in the whole life history. Thus, *e. g.*, in the alternation in certain Hydromedusae of a Polyp, producing asexually, and a Medusa, producing sexually, the Medusa is the terminal stage in the whole history, and the egg cell the beginning of it; the Polyp is simply an interpolation.

Claus had concluded (1885), in discussing alternation of generations, and particularly metagenesis: "The development of the two, three, or numerous generations can be a direct one or can depend upon a more or less complicated metamorphosis, and even so the relation of the nurse to the sexual generation can correspond sometimes to animal forms (*e. g.*, *Salpae*) which nourish themselves similarly and represent a similar stage of organization, and sometimes

correspond to the relation of larva and sexual stage (*e. g.*, Medusæ)." Thus Claus considered the nurse or Polyp individual to be a larva with the power of asexual reproduction, and the Medusa, which procreates by ova, to be the adult condition. This view has been advocated and elaborated particularly by Brooks (1886), from a careful analysis of the life history of the Narcomedusae and Trachomedusae. This is the same as the idea that we have just reasoned out, though from a point of view different from that held by Claus and Brooks; it is perhaps the more convincing when from such different starting-points the same goal should be reached.

But when Claus maintains that in the case of the Salpae the metagenesis is conjoined with direct development, we can safely say, by comparison with the other Tunicates, that such development is secondary among them, that the ancestors of the Salpae had originally indirect larval development. Further, the embryology of the Salpae is foetal, with the formation of particular foetal membranes, and we shall show that this is never continuous development. Accordingly, we would say that all cases of metagenesis have originated from larval development, and that asexual reproduction is limited to an immature or larval stage. Metagenesis by definition cannot be associated with direct continuous life cycles.

Now it will be recalled that metagenetic development implies one or more breaks in the continuity of the ontogenetic process. So far we have considered only cases where there is a succession of well-marked and clearly demarcated separate individuals in the life history. The term metagenesis has generally been restricted to just such cases. But logically we must go further and include under metagenesis all larval development in which there is discontinuity of organs and processes, that is, where certain larval organs

become lost and do not go to form parts of the adult. Beard (1893) was the first to argue from this standpoint. He reasoned from the relations in such larvae as the *Pilidium* of Nemertini and the *Bipinnaria* of Star-fishes, where the adult appears to arise as a bud from the larva in that it develops from only a restricted portion of the latter. He cites the case of the *Bipinnaria asterigera*, according to observations of Johannes Müller, where the young Star-fish dislocates itself and the larva continues to pursue an independent existence, though without further growth or reproduction. And he mentions the cases of Insects with complete metamorphosis, where the adult differentiates from only restricted portions (imaginal discs) of the caterpillar. All these he gives as examples of asexual generation upon the part of a larval form, alternating with the sexual generation by the adult; the part of the larva which does not transform into the adult being regarded as the parent of a bud which is the adult.

It seems to me that there can be no question of the correctness of Beard's view in this matter, and we might express it: all discontinuous larval development is metagenetic, in that the adult is formed asexually, by budding, from the larva. This has long been admitted as the most probable interpretation of the growth of the Nemertine from the *Pilidium* larva, where only a small portion of the larva goes to form the adult, simply four thickenings of the ectoblast. But embryologists generally have failed to see the wide application of such a conclusion. Frequently the greater part of the larva changes into the adult, even in discontinuous development, as in the metamorphosis of the tadpole into the Frog, where only the horn teeth and the external gill filaments are thrown off. But in most larval development, all but the continuous metaplastic development that we defined earlier in the chapter, there is a discontinuity

in the history of differentiation, in that certain larval structures do not take part in the production of the adult; such parts are then peculiar to the first individual, larva, of the cycle. Here is then clearly asexual reproduction, budding, on the part of the larva. It is indeed difficult to understand why the development of a holometabolic Insect, where the adult arises as virtual buds from the larva quite as fully as does the Nemertine from the *Pilidium* larva, should ever have been regarded as other than a process of metagenesis.

Even in the case of the Trochophore larva of Annelids Woltereck (1904) has demonstrated that a considerable portion of the larva becomes lost during the metamorphosis. He has shown that such discontinuous organ-formation, which he calls cenoplasia in distinction from metaplasia and orthoplasia, may be in two ways: by what Kleinenberg (1886) called substitution, in which "the original organ experiences no progressive metamorphosis, but dies, while a new formation, which cannot morphologically be derived in any way from the preceding, arises alongside of it and takes its place." And by what Woltereck himself calls "reservation," or the disposition in certain organs of the larva of living material destined to form adult parts, but which remains dormant until the larval stage has reached its end. Which of these processes is the more general, and whether both may not be concomitant, we cannot say, for observations upon the metamorphosis of larvae are very few, because difficult to institute.

All discontinuous development of the larval type is metagenetic, that is, implies in the life cycle a succession of individuals, usually two, the second of which is to be regarded as produced asexually by the first. This first individual is a larva, and it makes no essential difference in our idea of metagenesis whether the adult detaches itself from this

larva and the latter continues to live on, or whether almost all of the larva is consumed in the formation of the adult. In all these cases there is similarity in the association of larval development and discontinuity of process, so that the larva can be considered in them all as an individual that reproduces the adult asexually.

And accordingly we have to distinguish very sharply between two kinds of larval development. Larval development in a continuous ontogenetic cycle is metaplasia; the larva is perfectly continuous with the adult, there is no break between them, and there is no asexual reproduction on the part of the larva. But larval development in a discontinuous ontogenetic cycle is metagenesis; all organs of the larva are not continued into the adult, and that portion which does not change over into adult structures can be considered a first individual that produces a second by budding.

Here attention may be directed to one consideration that at first sight contains an apparent contradiction to the argument just presented. Haeckel (1866) distinguished between metagenesis, where one individual reproduces asexually and another one sexually, and strophogenesis, where one and the same individual generates at different periods sexually and asexually. Good cases of strophogenesis are found in certain freshwater Turbellaria (particularly the Microstomida); in *Lumbricus trapezoides* and the Naididae among Annelids; and, according to Curtis (1902), in *Planaria*. The objection would be in this wise: strophogenesis shows an alternation of sexual and asexual generations, and so far is like metagenesis, yet is not associated with larval development. But this is no exception to our general contention. For strophogenesis is discontinuous development, in that more than one individual composes the ontogenetic cycle: an individual produces asexually one that produces eggs, even though either individual may reproduce in both

ways. The development of any one kind of individual in strophogenesis may be direct, but the cycle is discontinuous, and for this reason any individual, when it first reproduces, which seems to be always asexually, may be considered an immature stage if not precisely a larva.

This account of metagenesis should not close without a reference to the recent view of a botanist, Chamberlain (1905). He states: "Since zoologists do not recognize in animals an alternation of generations comparable with the alternation of gametophytic and sporophytic generations in plants; it may seem presumptuous for a botanist to propose any theories. . . . In short, the theory is this: the egg with the three polar bodies constitutes a generation comparable with the female gametophyte in plants; similarly, the primary spermatocyte with the four spermatozoa constitute a generation comparable with the male gametophyte in plants. All other cells of the animal constitute a generation comparable with the sporophytic generation in plants, the fertilized egg being the first cell of this series." It will be recalled that botanists find in the series of liverworts, mosses, ferns, gymnosperms and angiosperms a succession which they regard as a racial metamorphosis from the earlier condition in which the gametophyte generation is the prominent one, to the later one where the gametophyte is much reduced and the sporophyte is the prominent generation. Their idea is that all of these plants show an alternation of sexual and asexual generation, a gametophyte alternating with a sporophyte. The gametophyte is defined as the producer or bearer of the gametes (macrospore, spermatozoid), while the sporophyte begins with the spore (fertilized egg) and is associated with its development.

But such a kind of alternation of generations is not paralleled in animals, for the reason that in no known Metazoan, not even the most primitive, is the maturation period

of the germinal cycle carried out in an individual separate from that in which the rest of the cycle takes place. Unless an act of asexual generation intervenes in the life cycle, a process of budding or fission, there is no alternation of generation in animals, but the germinal and somatic cycles constitute an unbroken and concurrent whole. The argument that Chamberlain adduces, the similarity of the maturation processes in Metazoa and Angiosperms, shows simply a correspondence of their germinal cycles, and does not in any way demonstrate the occurrence of successive gametophyte and sporophyte individuals in animals. And, as a matter of fact, the only approximately exact agreements between these particular plants and animals concern the stages of the reduction divisions in the germinal cycles, those cell divisions where the chromosomes become reduced to one-half of their normal number. But in the Angiosperms, where only two cell divisions follow this one, to complete the germinal cycle, in the lower plants there is a large number of succeeding cell divisions, while in all Metazoa invariably only one follows the reduction division. Therefore the more primitive plants differ most widely from the Metazoa in this process, and hence the greater agreement of the higher plants with the Metazoa must be a secondary convergence, and in no way date from the time when animals and plants arose from a common ancestor. The primitive and most usual condition in animals is that where the whole germinal cycle is completed within one somatic individual, and for these reasons the animals seem not to have any process of metagenesis comparable to the alternation of gametophyte and sporophyte in plants.

D. EKDYTIC DEVELOPMENT, VIVIPARITY AND OVIPARITY

As ekdytic ontogenetic cycles I propose to call all examples where, contrary to larval development, the earlier

stages of the organism are not freely locomotor but sedentary, undergo their differentiation within a circumscribed space, and thereby are induced to form special annexes for protection, respiration, and sometimes excretion and nutrition. This kind of development is discontinuous because such annexes are thrown off at birth, and are not continued as, or modified into, parts of the adult. Ekdytic development rightly interpreted includes both cases of intrauterine (foetal) development, and also any development within an egg shell where special membranes are formed and become later discarded. This is a moult, ecdysis, of living parts.

Just at this place should be considered the relation of oviparity to viviparity in sexual reproduction. Oviparity is that condition where the daughter individual separates from the mother in the stage of the ovum, or in an early cleavage stage; we say the young is born as an egg. Viviparity, where it remains in the mother's body during a longer or a shorter period of its subsequent history, and is born in a relatively advanced stage of development. These are, then, conditions of the parent rather than of the offspring, though with influence upon the ontogenetic cycle. Sometimes there is an alternation of viviparous and oviparous parents, as in some Dicyemida, Branchiopoda, Aphidae and Trematoda. Or again the same individual may produce eggs and embryos at successive periods in its life; so first Leydig (1867) saw in one ovary of an Aphid one egg tube producing viviparously, another oviparously. A very striking example of this is found in a group of rhabdocoele Turbellaria, the Eumesostomida, according to the reseaches of Bresslau (1904) and Sekera (1904). In these forms subitaneous (Summer) eggs develop viviparously within the body of the parent, then leave it by breaking through the body wall (usually near the eye region); after which the wound is

healed and the parent lays latent (Winter) eggs from the genital passages; whether these subitaneous eggs develop parthenogenetically appears not to have been decided. Therefore the state of oviparity does not always exclude viviparity.

The greater number of Metazoa are oviparous, so that viviparity appears the exception. Of those species that are viviparous it is most usual that every individual is viviparous throughout its procreative cycle. Oviparity and viviparity are closely allied, and the latter is dependent merely upon a longer retention of the developing egg within the body of the parent. In fact no sharp distinction between the two can be made, for the young may be laid in the one cell stage, which is oviparity in the strict sense; in the stage of early cleavage (some Rotatoria), or late cleavage (Birds), or in a more (Mammal) or less (Shark) pronounced stadium of foetal development, or even be deposited in the full-formed condition (the redia generation of Trematodes). Degree of complexity of the genital organs and degree of viviparity are more or less, not always, associated. And whether the young separates as an egg cell from the parent, or as an embryo, is to a certain extent dependent upon its position within the parent; but this again is not always true, for the egg cells of certain Annelids and Nemertines force their way out of the body-wall of the parent, as do the embryos of the Eumesostomida.

On account of its rarity, particularly in the lower groups of the Metazoa, viviparity is certainly a secondary condition. And the general opinion is undoubtedly correct, that its physiological importance lies in economy of the number of offspring, and greater chance for their survival.

Now, oviparous development may be either continuous, as in the Earthworm, or discontinuous, as in many Insects. But it is clearly erroneous to speak of viviparous develop-

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ment as direct and continuous, when the embryo forms structures, such as the amnion and allantois, which do not transform into adult parts. That is to say, certain growth energies of the embryo are discontinuous in that they produce some structures that have only a temporary use. Analogous structures, the amnion and serosa, are frequently found in oviparous development, as in Arachnids, Insects, Birds and Reptiles. In the latter cases such membranes arise within a hard egg shell or chorion, outside of the body of the mother; in the former cases, within this body. The main factor in the formation of all such membranes appears to be early development within a circumscribed space, with exclusion from general environmental media. Because oviparity and viviparity may agree in the possession of ekdytic membranes and of enclosure of the embryo, it is a matter of little importance whether the embryo develops within an egg shell or within a uterus. And for this reason I would propose to consider both conjointly and to include both under the name of ekdytic development.

There is a great difference between this ekdytic development and the metagenetic. The ekdytic is characterized by a non-locomotor embryo that forms temporary membranes mainly for purposes of respiration and excretion. Metagenetic development shows a free, motile larva, the temporary organs of which are mainly locomotor. These two kinds of discontinuous life cycles are conditioned by opposed modes of existence, the one spacially circumscribed, the other free, and therefore can have no causal connection. Beard is then correct in classing foetal development as discontinuous, but wrong altogether in regarding it as a form of larval development. Free life with embryonic habitude different from the parent's has led to larval development, and through it to metagenesis; sedentary life of the embryo, with absence of locomotion, has originated ekdytic develop-

ment. Both are essentially amphibiotic, but while the larva in metagenesis is always free, the adult free or not, the embryo in ekdytic development is always quiescent, and the adult locomotory. And there is to be found still another difference between the two. With a pronounced larval development the power of locomotion is for actively seeking food. But in ekdytic development the embryo either gets nourishment from the mother, as when it develops *in utero*, or else stores up within itself the necessary quantity of food substance (yolk). Accordingly, the "transitory nervous system" described by Beard in foetuses of Vertebrates, would, if it really occurs, be not a reminiscence of a larval nervous system, but rather one induced in connection with the formation of foetal membranes.

But the cardinal difference between ekdytic development and metagenesis remains to be mentioned. In the former the ontogenetic cycle is completed within the lifetime of one individual, and is without asexual generation; in the latter it includes two or more individuals, one or more of which generate asexually. Here is where Beard made a radical mistake in arguing that intrauterine growth implies an asexual generation, and that the adult arises as a bud of the foetus. This was a suggestive thought in the attempt to relate diverse phenomena, but breaks down upon examination. The mammalian embryo certainly looks at the start, in the stage of the embryonic shield, like a bud placed upon the larger germ vesicle. But it is from its commencement more differentiated, more complex, than this vesicle, whereas a bud is at the start always simpler than the parent from which it abstricts. Its later foetal membranes, the amnion and chorion (serosa and allantois), are outgrowths from the embryo, not the embryo from them. Therefore these foetal membranes, and such parts of the germ vesicle as are not concerned in the formation of the embryo, are to be re-

garded as portions of the embryo that it casts off at birth, and not separately or collectively as an individual which produces the embryo by budding. Equally, ekdytic development within an egg shell, as in a Bird or Insect, shows the membranes as outgrowths of the embryo. Accordingly, there is no alternation of sexual and asexual generations in discontinuous ontogenetic cycles of the ekdytic type.

Ekdytic development would be continuous development were it not for the formation of certain structures that are not continued into the adult stage.

Ekdytic development may occur in the same cycle with metagenesis, as in holometabolic Insects, those with a complete metamorphosis. Here the embryo within the egg shell is provided with foetal membranes, which it casts off at birth; then it is a larva, and this larva, when in the quiescent condition of the pupa, produces the adult (imago) asexually; the adult then reproduces sexually. Such an Insect has then four modes of life, and so might be called tetrabi-otic: at first it is immovable within the egg shell, then locomotor as a larva, quiescent again as a pupa, finally volant as an imago. When one wishes to see for himself some of the mysterious examples of complicated life cycles he assuredly does not have to go far to find them.

It is even possible for a larva to become a foetus by its retention within some brood-chamber of the parent, as in the case of some Sharks and Molluscs, and of *Capitella* among Annelids. But in such cases it is probable that strictly larval organs, which are specialized for locomotory purposes, would not metamorphose into foetal membranes, that are mainly for protection and respiration, but would be first lost, then replaced by the latter.

Faussek in 1893, in a Russian paper not accessible to me (compare his contribution of 1904), and Houssay (1900) have called attention to a supposed parallelism between

viviparity and parasitism, in that an intrauterine foetus might be considered a parasite within its mother. But this is simply a loose analogy. For an entoparasite is abnormal from the standpoint of the host and directly injures the latter, while the possession of a foetus is so far normal in viviparous animals as to be absolutely essential for the continuance of the race. For this reason a foetus cannot be considered an entoparasite, but rather a commensal.

E. HETEROGENESIS

The third kind of discontinuous ontogenetic cycle is heterogenesis. This is a succession of sexual generations in such manner that amphigony, development by a fertilized egg, alternates with parthenogenesis, development by an unfertilized egg. Like metagenesis it is discontinuous development extending over two or more individuals, but, unlike it, all the generative processes are sexual. To clear the ground for the following discussion it will be first necessary to mention the various definitions that have been given to parthenogenesis and heterogenesis.

The word heterogeny was first introduced by Leuckart (1853) for cases of alternation of amphigony and parthenogenesis, as well as those of alternation of dioecism and hermaphroditism. Later (according to Braun, 1893) Leuckart restricted this term to the alternation of dioecious and hermaphroditic generations, and used the word alloio-genesis for the other kind of alternation. But Haeckel had previously (1865) applied the word alloeo-genesis in a very different sense. Balfour (1885) used the term heterogamy as equivalent to heterogenesis in its now generally accepted sense, *i. e.*, the alternation of generations producing amphigonously and those producing parthenogenetically; but now heterogamy has come to be applied to cases of reproduction through dissimilar gametes. Owen (1849) first brought in

the word parthenogenesis to mean alternation of generations. But at the present time, following the example of von Siebold, it is limited to development of egg cells where there is no fertilization. We shall use parthenogenesis in von Siebold's definition, and heterogenesis in the generally accepted significance already mentioned.

Parthenogenesis may be (1) partial, that is, not leading to development beyond an early embryonic stage; or (2) complete, with development up to the adult condition. This complete parthenogenesis may be (a) exceptional and occasional, or (b) normal and regular. In regard to the sex of the individuals produced parthenogenetically there are the following known conditions: (1) both males and females are produced (amphoteroky); only one sex is produced (homoparthenogenesis). In the latter condition only males may result (arrenotoky), or females only (thelytoky). Phillips (1903) has recently given a very useful and full review and classification of the different kinds of parthenogenesis, from which this classification has been taken. Occasional and incomplete parthenogenesis we need not consider, nor yet parthenogenesis produced artificially.*

Normal heterogenesis is found notably in certain Insects, phyllopod Crustacea, Rotatoria, Trematoda and a few other forms. The alternation of generations of the Trematodes was originally interpreted by Steenstrup as metagenesis, but now it seems proven that all generations but the last in these complicated life cycles are cases of parthenogenesis, the cycles as wholes therefore heterogenetic. So Braun (1893), states: "Upon the morphological evaluation of the so-called

* So far as is known to me all parthenogenesis produced by artificial means is incomplete, that is, the embryo does not develop into the adult condition. Such experiments were, to my knowledge, first successfully carried off by R. Hertwig on Sea-urchin eggs stimulated by strychnine. The results of these and later experiments have not helped much to elucidate the normal process of parthenogenesis.

germ cells of the sporocysts and redias there can no longer be any doubt; repeatedly attention has been called from different sides to their great resemblance to the germ cells of the germ glands of sexually mature Trematodes, a resemblance that concerns not only the appearance of the cell body and the nucleus, but also the size—they are germ cells that develop without fertilization, accordingly parthenogenetically.”

The probability of the occurrence of parthenogenesis seems to be proportioned inversely to the number of male individuals. There may be an actual smaller number of males, as in Rotatoria and Phyllopoda; or else the ova may be so placed as to exclude their chance of fertilization, as particularly in exquisite parasites; or they may develop within the body in such manner that spermatozoa cannot reach them. For this reason it may be that lack of males or their infrequency is the main cause of parthenogenesis, and not intrinsic differences in the eggs; but we will return to this point.

Just as we have found that alternation of sexual and asexual generations may occur in the same individual (strophogenesis), or be extended over several individuals (metagenesis), so heterogenesis, which is the sequence of amphigony and parthenogenesis, may occur in one individual or be continued over more than one. Thus in the Phyllopods, Rotatoria, Aphids and some others the same individual may reproduce first parthenogenetically then amphigonously. In the digenic Trematodes, on the other hand, these two kinds of sexual reproduction are distributed over different individuals. Again, there are complex cycles known where some individuals produce only parthenogenetically, others in this way and also amphigonously. In the case of Rotatoria the same individual produces parthenogenetically a number of individuals, then one or more by means of fertilized eggs.

In such a case parthenogenesis accompanies a relatively immature stage of the organism, or rather, accompanies the early portion of the period of generation. This is also the case with digenic Trematodes, and with those Insects where heterogenesis extends over several individuals. An apparent exception will be considered later.

The fertilized egg is then the beginning of each heterogenetic cycle, because produced by the individual that comes latest in the cycle or in the stage of greatest maturity. Therefore for heterogenesis, as for metagenesis, the initial stage is the fertilized egg, and the terminal one is the individual that again procreates by fertilized eggs. Reproduction by parthenogenesis would be an interpolation in the cycle. This would probably be true whether the cycle include one or several individuals. But, unlike metagenesis, heterogenesis may in some cases have arisen from direct development; this might well have been the case in the Rotatoria. I think it probable that in almost all cases of heterogenesis development by unfertilized eggs is a characteristic of the earlier germ cells, not of the ones formed latest. Now, von Baer (1864) applied the term *paedogenesis* to parthenogenesis occurring in a larval form. Consequently if we amplify von Baer's definition of *paedogenesis* to include parthenogenesis at any immature stage, irrespective of whether that immature stage is a larva or not, then parthenogenesis would practically become equivalent to *paedogenesis*.*

Conversely, we might conclude that any individual generating by unfertilized eggs is probably not a fully mature stage. This condition would then be in heterogenesis an

* In the case of the Honey Bee, on the theory of Dzierzon (1852), it is well known that the adult queen may lay at the same time, or rather in rapid succession, both fertilized and unfertilized eggs, and that both of these are capable of complete development. This is not heterogenesis in the strict sense, however, so not an objection to the view just stated.

interpolation in much the same way as asexual generation is in metagenesis.

Heterogenesis would seem also to be generally accompanied by amphibiosis, but amphibiosis of such a kind that the different individuals or stages would differ not so much in habit as the environmental conditions of the two would differ. It results often in seasonal dimorphism, a phenomenon to which we will return at another place.

In the most painstaking and thorough analysis of heterogenetic life cycles yet undertaken, Weismann (1879) has studied these questions with particular reference to modes of life. He examined particularly phyllopod Crustacea of the freshwater. Before his time the occurrence of two kinds of eggs in certain animal groups had been determined, and it was found that one kind, the "Winter" eggs, require fertilization, and the other, the "Summer" eggs, develop without fertilization. To these two kinds Weismann applies the terms "latent" and "subitaneous" respectively, and the females that produce them he calls correspondingly latent and subitaneous females. These eggs may or may not appear structurally different, though frequently the latent eggs are larger and with a thicker chorion. Now Weismann finds the essential difference between them to consist not in morphological characters, nor yet in characters of fertilization, but rather in that the latent eggs do not immediately develop into an embryo, but remain quiescent for a time like a Protozoan that is encysted.

Weismann states as some of the results of a long series of observations: "The sexual generations can contain together with male and female sexual individuals also a greater or smaller number of unisexually reproducing parthenogenetic females, but not in all Daphnoids do the sexual females under normal conditions proceed to parthenogenesis after the generation of latent eggs. The allotment of the two

female modes of reproduction to two kinds of individuals is varyingly precise, according to the generation and the species; the first generation of all species reproduces never sexually [amphigonously] and in some species the individuals of all generations born parthenogenetically are incapable of producing eggs that need fertilization (*Moina*), just as, on the other hand, in some species (*Polyphemus*) sexual females always produce only eggs that require fertilization and do not later proceed to parthenogenesis."

He accepts the view of Claus (1876) that forms more or less similar to the existing Estheridae were the ancestors of the Daphnidae. The former are not heterogenetic and have only one kind of eggs, which he holds to be comparable with the latent eggs of the Daphnids. The modern Daphnids have a direct development, and Weismann attempts to explain how the heterogeny in this group has arisen from the condition maintaining in the Estheridae that have larval development. So he reasons that in the Daphnids the reproductive cycle was originally monocyclical, extending from the fertilized latent egg to the adult that produces eggs requiring fertilization again; and that therefore latent eggs and latent females are primitive, and subitaneous eggs and females secondary.

Weismann reasons that the commencement of the polycyclical development of the Daphnids is to be sought in the ovogenesis, in the differentiation of the ova into subitaneous and latent eggs. "The genera *Apus* and *Limnadia* produce, as most of the Phyllopods, only one kind of eggs, namely, latent eggs, but these can develop both parthenogenetically and by fertilization; in *Apus*, even in one and the same species, in *Limnadia* at least in different species. The dropping out of fertilization can therefore not be the moment which has conditioned the subitaneous development, and, conversely, fertilization not the moment which conditions the

latency. Further, two species of *Artemia*, *A. salina* and *A. fertilis*, possess two kinds of eggs, subitaneous and latent eggs, and both can develop as well parthenogenetically as after fertilization." The key to the polycyclical development Weismann holds to be a process of natural selection: with an elongation of the period of the colony of individuals opportunity is presented for the production of successive broods in the same season, and this condition would be maintained by selection on account of its importance in the perpetuation of the species. Some of the eggs remained Winter eggs with latency of development; others by omitting this rest period in their development, by immediateness of differentiation into the embryo, became Summer eggs.

For all the many suggestive conclusions concerning the Phyllopods the reader must refer to the original memoir by Weismann. One point may be emphasized: that the phenomenon of latent and subitaneous eggs is distinct from parthenogenesis and heterogenesis, though it may be associated with them. This comes out clearly from Weismann's reasoning.

But while such occurrence of two kinds of eggs may not, and probably has not, any immediate connection with parthenogenesis, yet it must be the lack of males that has brought about parthenogenesis rather than any process of differentiation of the egg cells. We have in mind the case of *Artemia salina*, which has both latent and subitaneous eggs, either of which is able to develop with or without fertilization. This observation is based upon the authority of von Siebold (1873). Perhaps this is to be explained in the words of Brauer (1893), that *Artemia* is "on the way to accommodate itself wholly to parthenogenetic reproduction." At any rate, in *Artemia* itself the rarity of the males is unusually striking; and in all cases of parthenogenesis males are absent during the period of procreation. The

real problem is then this: What induces rarity or absence of males?

Weismann showed that in the Daphnids with heterogenesis the first generation of females to reproduce do so always by means of unfertilized eggs. This is in agreement with our contention that parthenogenesis is a condition interpolated between the first and last stages of the ontogenetic cycle; it is a condition accompanying immaturity. But females of some species of Daphnids terminate their reproductive activity by the formation of subitaneous eggs; here, accordingly, parthenogenesis is an accompaniment of the most mature stage. This would appear to be an objection to our conclusion just expressed. But it need not be, for such females may not be the terminal individuals of their respective cycles.

Heterogenesis and metagenesis are quite distinct modes of discontinuous cycles. Yet in some animals they may be found together, and it is just such coincidence that has given rise to much confusion in the analysis of alternation of generations. But even when they occur in one and the same species they remain entirely different processes, just as do the processes of ecdytic development and metagenesis in the case of an Insect with complete metamorphosis. In the *Orthonectids*, according to the account of Julin (1882), there are, besides males, two kinds of females, cylindrical and flattened. The flattened females divide asexually into a number of pieces, each of which grows into a "primordial sac." Centrally placed cells of the latter produce, supposedly parthenogenetically, the two kinds of females. The cylindrical females so formed generate, supposedly by unfertilized eggs, the males. In these animals the occurrence of parthenogenesis has not been actually demonstrated; it has rather been inferred. But if it does occur, then here is associated metagenesis, the alternation of asexual reproduction

and sexual, with heterogenesis, the succession of amphigony and parthenogenesis. In the Dicyemids, on the other hand, at least according to the account of Wheeler (1899), only heterogenesis occurs and not metagenesis; but the older investigators, Whitman (1882) and E. Van Beneden (1882), have interpreted the processes differently. In one of the Hydromedusae, *Cunina proboscidea*, Metschnikoff (1886) states that unfertilized eggs develop by metamorphosis into Medusae that produce buds, and the latter become Medusae of a very different structure, generating by fertilized eggs. This very unusual process requires confirmation. Then, again, while the ontogenetic cycles of the Trematoda are for the most part heterogenetic, asexual generation of the sporocyst individuals alone, by fission as well as by budding, has been repeatedly observed (Braun, 1893, p. 806, gives a list of the known cases); here also then there is association of metagenesis and heterogenesis.

The conclusions reached present certain points of view that are of practical value to the student of racial histories. A form without asexual generation is, *ceteris paribus*, more primitive than one with it; one without parthenogenesis than one with it; and one with a continuous ontogenetic cycle than one with a discontinuous cycle. Both metagenesis and heterogenesis are cases of alternation of generations, and the life cycle in them is composed of more than one individual; but the third kind of discontinuous development, the ekdytic, is monocyclical. In any case of alternation of generations that individual which reproduces by fertilized eggs is to be regarded as the terminal one in the cycle; and an individual generating asexually, as well as one generating parthenogenetically, is to be considered a more immature individual, an interpolation into the cycle. The stage of the mature, fertilized egg is the end of the germinal cycle and the commencement of the somatic.

F. CYCLES IN PROTOZOA

In conclusion we may turn to the Protozoa, where the life histories are for the most part known far less completely than in Metazoa, and where they are frequently more complex. The Protozoan is comparable with both germ cell and body constituent of a Metazoan. Nothing exactly similar to sexual reproduction is found in these unicellular forms, for the reason that in them conjugation has usually no immediate connection with reproduction. Conjugation of unlike spores (gametes) is the nearest approach to the sexual reproduction of the Metazoa. Therefore all the modes of reproduction of the Protozoa, binary fission, budding and fragmentation, are comparable to metazoan asexual generation. As in the multicellular animals, so in the Protozoa, two main kinds of ontogenetic cycles may be distinguished, the continuous and the discontinuous.

Continuous cycles occur in numerous Flagellata and Ciliata, with generation by binary fission alone, and in most Suctoria, with generation by budding alone. Whether there are any forms that reproduce by fragmentation alone I believe is not known. In binary fission the parent ceases to exist as one entity after the daughter individuals have formed, but this is not the case in budding. In fission the two offspring may not differentiate their various structures until they become separated, but more usually they do so to some degree of completeness while still connected; the former process is probably the more primitive.

Discontinuous cycles, those extending over a number of individuals, are characteristic of very diverse groups of the Protozoa, particularly of Sarcodina and Sporozoa. There may be a succession of binary fission, budding and fragmentation in manifold sequence; and the life cycle extends of course over as many individuals as there are different kinds

of generations. Which individual of the series is the starting-point depends accordingly upon what mode of reproduction is regarded as the most primitive. Budding is for many good reasons to be left out of consideration, so that a decision must be made between binary fission and fragmentation. In the previous chapter we decided for the latter. From this standpoint spores (gametes) would be the first individuals of any cycles possessing generation by fragmentation, and consequently the individuals that produce them the last stages of the cycle. Individuals arising either by budding or fission would then be interpolations between these two stages.

Like metazoan metagenesis, the whole sequence would be discontinuous development, with binary fission and budding restricted to the immature stages. Because fragmentation, spore-formation, is of all protozoan modes of generation the one most like the sexual reproduction of the Metazoa, there is still another correspondence: the initial stage in both animal groups is a gamete, a spore in the case of Protozoa, an ovum in the case of Metazoa. Such life cycles have then a very close correspondence to metazoan metagenesis.

G. POLYMORPHISM OF INDIVIDUALS

Under polymorphism is generally understood the presence of more than one kind of individual in a species, and such a species would be polymorphic. While the word itself etymologically expresses differences of form only, we shall include in it differences of color and differences in mode of life. As we shall find, it is particularly the last condition that is the essential characteristic of polymorphism.

The main phenomena shown by animals with regard to states of polymorphism may be classified as follows:

I. Monomorphism. All the individuals alike in the same and successive generations, *i. e.*, no polymorphism.

II. Polymorphism.

1. Between individuals of the same generation.
 - a. Between male and female individuals (sexual dimorphism).
 - b. Between reproductive and non-reproductive individuals.
 - c. Between different kinds of males, or different kinds of females.
2. Between individuals of successive generations.
 - a. Between sexual and asexual individuals.
 - b. Between sexual individuals, and then:
 - (1) between corresponding unisexual individuals,
or
 - (2) between dioecious and monoecious individuals.

Delage (1903, p. 180) proposes the term metagenetic polymorphism for the condition we call polymorphism between individuals of successive generations, and ergatogenic polymorphism for that kind obtaining between individuals of one and the same generation. His second term is not a happy one, because, while it correctly implies a state of division of labor, it indirectly suggests that such division of labor is not also characteristic of metagenetic polymorphism. And his first term also is not well chosen, because the polymorphism of successive generations may be associated with heterogenesis quite as well as with metagenesis. And under the name of oecogenic polymorphism Delage includes individual variation produced by environmental change; but fluctuating individual variation is a condition quite different from polymorphism as the latter is generally comprehended, for the latter is a fixed, and not a fluctuating, condition. For these reasons it seems best not to adopt Delage's terminology.

Monomorphism, or absence of polymorphism between in-

dividuals of the same generation, is probably a secondary and not a primary state in the Metazoa. It is found when all the individuals are unisexual and of the same sex, as in some parthenogenetic generations, and in some of those species where the individuals are hermaphroditic. The first of these cases is undoubtedly not primitive, because parthenogenesis is secondary; and we have given reasons to show that a hermaphroditic condition is also not primitive. But monomorphism of successive generations is more primitive than polymorphism of successive generations, because the former is associated with continuous development and the latter with discontinuous.

The commonest form of polymorphism is the distinction between male and female individuals of the same generation; this is sexual dimorphism, and it always occurs when the species is not hermaphroditic. It is a distinction between reproductive individuals, females, and fertilizing individuals, males. Usually there is then but one kind of male and one kind of female. But sometimes there are different kinds of female individuals in the same generation, as notably in many Hymenoptera among the Insects; then it is the rule that one kind, the queens, are the normally reproductive individuals, while the others, the workers, which again may be of different kinds, either possess reproductive organs in a very rudimentary condition and so do not form eggs, or else are capable of sexual generation. For one species of Ant, Wheeler and McClendon (1903) have described the occurrence of two kinds of queens. The division of labor here is not so much between exclusively reproductive and exclusively non-reproductive females, as rather between females whose main value is reproduction and others whose main value is the care of the young: it is really a distinction between mothers and nurses. More rarely the males of the same generation are of different kinds, as in the Termites

among Insects, where there may be three kinds of males or three sorts of females, each one of which carries out some particular duty for the good of the colony. In certain Flies also there is dimorphism of males, as, too, is the case in Spiders of the family Attidae (and probably certain of the Theridiidae). In a Spider of a different family, the *Lycosa inhonesta*, which is found over most of North America, two kinds of females were described by me, which differ mainly in size, but appear to have identical conditions of life.

This sexual dimorphism, distinction of two sexes, rests upon a division of labor, the males carrying the fertilizing germ cells and the females the reproductive cells. This is the fundamental condition of this kind of polymorphism. As a rule the egg cells take longer to mature than the spermatozoa; they are always larger, and these differences are expressed more or less in the differences of the individuals containing them. As a rule the male is more embryonic and of shorter duration of life. In some of the higher animals, notably among Birds and Mammals, and in some of the lower forms also, the sexes frequently differ likewise in mode of life, and Cunningham (1900) is probably correct in ascribing some secondary sexual differences to the influence of different modes of life. But he goes decidedly too far in attempting to explain all secondary sexual differences on this basis, for there are many animals with such distinctions of structure and color, but where the two sexes lead nearly the same kind of existence. Cunningham's theory, however, may be in closer accord with the phenomena than the sexual selection theory of Darwin (1886), or than Wallace's idea (1903) of the greater strength and vigor of the male. And certainly division of labor is the underlying cause of the polymorphism of different castes of individuals of the same sex in the same generation. In the entoparasitic Crustacea the female is large but very degenerate,

owing to her exquisite parasitism, while the male is more embryonic, much smaller and free.

Individuals of the same generation may show also a distinction between asexual and sexual forms, meaning by the latter not those with rudimentary reproductive organs, so not such cases as the workers of Bees and Ants, but those entirely without such organs. Such are certain marine Bryozoa, with the sexless Avicularia and Vibracularia; plumularian Hydroids with non-reproductive Nematophores; Siphonophores with sexless nutritive, tactile and defensive Polyps. All such cases appear to be restricted to animal species forming colonies; the sexless individuals are neither male nor female, and have not even the power of asexual reproduction, the latter condition being associated with polymorphism of successive generations.

Then there may be polychromatism of individuals of the same generation, independent of sex. This is so in some species of the American Screech Owls, *Megascops*, where some individuals are gray through life and others are red. And in an American Newt, *Plethodon cinereus*, where some individuals, and here again independent of sex, are uniform blackish, others with a red dorsal stripe. These are individual differences independent of the sex and age of the individual, and are of regular occurrence in every generation; they are of course not to be compared with albinism and melanism, which are expressions of extremes of individual color variation.

But of wider interest are the cases of polymorphism between individuals of successive generations. In metagenesis sexual individuals of one generation alternate with asexual ones in the next; in heterogenesis, parthenogenetically reproducing females with such as reproduce by means of fertilized eggs. In the cases of metagenesis the sexual individuals may differ from the others merely in the presence of

mature germ cells and of reproductive organs, but more frequently they differ in other structures as well. Or there may be distinct males and females in one generation alternating with hermaphroditic individuals in a following; this is a rare case, but was discovered by Leuckart (1887) in certain Nematodes. A third kind of successive polymorphism is the difference between a male of one generation and a male of the next, or between a female of one and a female of the next; this may be associated with heterogenesis, as in the Phyllopod Crustacea, where the females reproducing parthenogenetically may lack copulatory organs or evince a different ovarian structure (Weismann, 1879). But frequently this third kind is not in combination with heterogenesis, and is then known as seasonal dimorphism, individuals produced at one season differing from those born at another. This may be a difference merely of color, as in some Butterflies and some other Insects; or even of both form and size, as in some Rotatoria.

The consideration of the phenomena of polymorphism, which we have treated only summarily and in all brevity, shows that there is no immediate dependence of polymorphism upon modes of reproduction. In the Termites there is extreme polymorphism but only one kind of reproduction. The same individual, in a case of strophogenesis, may generate first asexually, then sexually, but it differs in structure in these two epochs of its life merely with regard to the degree of maturity of the germ cells. In cases of heterogenesis the females forming eggs that need fertilization usually do not differ from the females reproducing parthenogenetically. Hermaphroditic and dioecious individuals may alternate, but the mode of reproduction is one and the same. Then there may be great differences between individuals of the same generation that do not reproduce in any manner at all. The most general form of polymorphism,

sexual dimorphism, is founded upon a division of labor, the males bearing fertilizing germ cells and the females reproductive cells. All other types of polymorphism are also associated with a division of labor between the differing individuals, or with differences in environmental relations. In those Nematodes where hermaphroditic individuals alternate with dioecious ones, the former are parasitic, the latter free; differences between successive seasonal broods in Insects or Rotatoria clearly correspond to differences in seasonal environmental differences. Alternation of sexual and asexual generations in the Hydromedusae frequently coincides with succession of motile and sedentary life. This idea will be found upon reflection to be so well founded, so much in agreement with the phenomena of polymorphism, that it needs no further exemplification.

Polymorphism is accordingly a function, in the mathematical sense of the word, of division of labor between individuals. It is not necessarily either induced or modified by change in reproductive activities. Colonies of polymorphic individuals, as in a Siphonophore or Hydropolyp, arise by budding from one individual; but the polymorphism of these buds is not in any way due to this particular kind of development. On the other hand reproduction can be much more readily modified by polymorphism, in that certain individuals may become so specialized as to lose the capability of reproduction of any kind. Mode of life is of immediate influence upon both polymorphism and reproduction. The primitive condition in the Metazoa, reproduction by means of fertilized eggs, may become changed into parthenogenesis both by extreme parasitism and by seasonal change of the environment in free forms. And we have seen that metagenesis has arisen through the supplanting of the primitive continuous development by the secondary discontinuous, that is to say, by the interpolated

stage, the larva, taking up a mode of reproduction different from that of the adult.

These considerations make it evident that the old idea of alternation of generations must be split into its two main components, which are: alternation of different kinds of reproduction, and occurrence of structurally different individuals. These two sets of phenomena should not be confused, for they have no other common connection than that of response to varied environmental influences.

The characteristics of ontogenetic cycles and of polymorphism, when carefully analyzed, may be found of great service in determining racial descent.

CHAPTER V

VARIATIONS AND MUTATIONS

AN individual is said to possess variation when it shows a character not present in its ancestors.

Two kinds of variations were distinguished by Darwin (1859, 1868): individual or fluctuating variations, and sports, the latter being better known at the present time as mutations. The differences between the two have been analyzed by no one more fully than by de Vries (1901), who compares them as follows: the individual or fluctuating variations are those differences constantly present in any species, and which may be grouped in a single curve of mathematical probabilities. Most of them approximate to the mean, successively fewer to the extremes. The especial characteristic of this kind of variation is that it is omnipresent and gradual, and it is exhibited particularly in gradations of number, dimensions, and intensity of color, that is, in gradations of degree. When a sufficient number of individuals are examined, their differences may all be plotted in a single, uninterrupted mathematical curve. The degree of such variation may vary with different species and different characters, but it is always a gradual series from one extreme to the other.

Mutations are what the earlier naturalists called chance variations, fortuitous variations, spontaneous variations and sports. Darwin recognized their occurrence, later Bateson (1894) and Scott (1894), while de Vries (1901) has studied them in a masterful manner. A mutation is a departure that is not connected by gradations with a mean,

and mutations cannot be plotted in a single probability curve. Mutations form a discontinuous series, and this is the main difference between them and the individual variations. Further, they appear to occur at certain periods (mutation periods), then in but a limited number of individuals, and not in all generations and individuals of a species. As de Vries expresses it, a mutation appears suddenly and without interposition of gradations. A mutation need not be a variation of large extent, but may be less in amount than the difference of the extremes in individual variation.

The same individual may show at the same moment of time both these kinds of variations, so that they are not mutually exclusive.

De Vries distinguishes three kinds of mutations: (1) progressive, the appearance of a character new for the race; (2) retrogressive, the complete disappearance or latency of a character; and (3) degressive, the reappearance of a character that had been in a latent condition. The last kind of mutation can be determined only by breeding experiments, whereas the others may be ascertained in some cases by other observational means.

Individuals that evince variation of the one kind or the other have been variously termed variations, varieties, geographical races or subspecies, sports, etc. But in order to avoid conflicts in terminology the word variation had best be reserved not for the individual possessor but for the condition or character that distinguishes it from other individuals of the same species. And further, it had best be limited to individual or fluctuating variation. An individual marked by such variation might then be called a variant, or fluctuating variant. This is not a new term, but has heretofore been used interchangeably for the possessor of either individual variation or mutation. The possessor

of a mutation is, in de Vrie's terminology, a mutant. This writer, as we have just seen, in distinguishing between three kinds of mutation, draws the line also between three kinds of mutants, namely, progressive, retrogressive and degressive. At the same time he classes the progressive mutants apart from the other two, because they are characterized by the possession of a new character, and calls them incipient or elementary species. The retrogressive and degressive mutants show mutations of latency or reappearance from latency, and de Vries classes them together as varieties, making the point that such varieties differ only in degree from elementary species. This is a particular use of the word variety for previously it had been employed, by most zoologists at least, for variants as well as mutants. These terms may be compared as follows:

	<i>Condition</i>	<i>Individual</i>
	Variation	Variant.
Mutation	Progressive...	Elementary species.
	RetrogressiveVariety
	Degressive	
		Mutants.

Variants may and probably do occur in every generation, mutants only during a period of mutation, and then only up to the time when many individuals show the mutation.

The criteria of variants, elementary species and varieties can in most cases not be determined by direct observation, for the reason that a mutation need not involve a greater perceptible difference than a variation. Perhaps in most cases, then, as de Vries has pointed out, only cross-breeding experiments, with analysis of the behavior of single characters in the resulting hybrids, can present the determination. Obviously this cannot be carried out for the great series of known fossil forms, nor yet for the great majority

of the living forms, particularly animals where such experiments are much more difficult than in most plants.

There can be no doubt that the modern statistical study of variation, on the lines set down by Galton (1869), is able to decide between variants and mutants. It becomes simply a mathematical question of the regularity and continuity of the percentage curves. But it should not be forgotten that geographical races, so important to the phylogenist, were recognized and named by systematists before the statistical methods were employed. The chief value of the statistical method is that it dispenses with the "more" or "less" and establishes its conclusions upon a greater series of comparative measurements, thereby lessening the chance of error. Of particular importance to the student of species is the working out of the so-called place-modes, or place-constants, a line of research in which the name of Davenport has become particularly prominent. By this is meant the mode or kind of variation exhibited by individuals within a certain portion of the geographical area of the species. When it has been computed for one such group of individuals, similar studies can be made upon individuals from other portions of the area, and so by statistical methods the geographical races be worked out and the distinction be made between variants and mutants. It comes to be a comparison of the resulting percentages, and the determination whether they compose gradated series or not.

The species defined by Linnaeus (1758), as those of the general systematist, are collective groups, including smaller ones; the species unit would be, de Vries urges, each progressive mutant race (incipient species). From this point of view the varieties and elementary species of de Vries would be the really important unit groups to the phylogenist. And thereby hangs a curious revolution of opinion. Those species describers, most numerous among

conchologists and ornithologists, who have been naming and describing each recognizable geographical race have won the name of "species-splitters" from their more conservative adversaries, the "species-lumpers." Many of the latter have gone so far in their criticism as to disregard the names and diagnoses of subspecies, and so to avoid the use of the trinomial nomenclature. But the statistical study of variation, as well as the analysis of the characters of hybrids, has demonstrated to the full the value of these fine distinctions of the species-splitters, and the relative unimportance of the work of the species-lumpers. It is of exceeding importance to recognize and name all the smaller geographical races, for they are the proper species units, some of them perhaps mutants, and thereby constitute the first groups, after the offspring unit, which the phylogenist has to consider in his synthetic studies.

When the process of heredity proceeds unchanged the ontogeny of one individual is just like that of its parent. When a change of the ontogeny occurs, so that the offspring comes to be different from its parent, we say that a variation has appeared in the offspring. This variation, it is thinkable, may have been produced: (1) by internal growth energies, (2) by external environmental influences, or (3) by a combination of both; and it is necessary to discuss which one of these is the most probable.

There is clearly, in the process of production of variation and mutation, some modification of the normal process of heredity. Since in a number of species it has been shown that all the adult individuals from one locality are not exactly alike, but show measurable differences in dimensions, color or some other character, it follows that the hereditary process of each such individual must vary correspondingly, even though the variation does not become perceptible until the stage of maturity. The origin of in-

herited variation or mutation is then a question of the origin of modification of the hereditary process.

The regularity of the process of heredity is quite comprehensible on the basis of the direct transmission of definite chromosomes in number, form and quality constant for the species. From cell to cell, from individual to individual, these chromosomes are regularly transmitted in a continuous progress, therefore a succession of similar individuals is quite understandable. One germ cell comes from a preceding one, to our knowledge is never formed from a specialized tissue cell, so that there is an uninterrupted passage of the germ plasm through the race. This is Weismann's idea of the continuity of the germ plasm, which we will paraphrase as the continuity of the chromosomes.

A variation to become inherited must then be referable to a modification of the energies of this germ plasm. The germ plasm is living substance of proved great importance in the metabolism of the cell. Though in a sense it appears, from microchemical researches, to be the chief agent in constructive growth processes of the cell, it equally appears to be incapable of life, or unable to act in a normal manner, when removed from the influence of other cell substances. The food required by a germ cell for its growth is obtained from without the cell, and must pass through the cytoplasm, in more or less changed condition, to reach the chromatin within the nucleus and there be elaborated into living substance and passed over to the cytoplasm in other form. This conclusion is drawn from both experimental and microchemical studies. So the oxygen required by the cell, and the water, must be obtained from without the cell. This is simply in agreement with the general principle that no body can increase in mass, circumambient conditions remaining unchanged, without accretions from outside. Therefore the germ plasm does not so much

create new substances as it changes substances brought to it. It and the other cell constituents are harmoniously and mutually interdependent, and the ultimate source of energies of these substances, all connected with the elaboration of living matter, is referable to external agencies because referable to food.

This being the case, the energies of the hereditary substance, the germ plasm, are clearly dependent upon influences of the environment. This conclusion is not at all in contradiction with the idea of the continuity of the chromosomes, as we pointed out in the preceding chapter. Therefore Weismann was in error when, to support his idea of the continuity of the germ plasm, he at first argued the energies of the germ plasm to be independent of body cells and of the environment generally. His supposition was both unnecessary for the view of the continuity, and also out of agreement with the phenomena. The ovum cannot elaborate its yolk substance except out of food substance received from without; the amount of its food substance will depend upon the state of nutritive metabolism of the individual carrying the egg cell; starvation of that individual will cause cessation of energy in the germ cell, and ligaturing of the blood vessels supplying the ovary will produce death of the egg cells. The results of observational experience teach that the germ plasm is not a little god, capable of self-existence without respect to external agencies, but is very intimately bonded to the latter. Whether the germ cell, as in the Sponges, be an amoeboid cell which wanders about in the body tissues, or whether it is immovably held in place by tissue cells, it is impossible that it can live and grow without receiving and reacting to stimuli from these tissue cells. The egg cells of many animals are set free in water before they commence to cleave into embryonic cells; how can we

say that the conditions in the water do not influence them? They will die if removed from the water, and develop abnormally if certain substances be added to or subtracted from the water. But the embryonic differentiation is a result of chromosomal activities, as we have seen, therefore changes in the medium must influence the germ plasm. Is not a well recognized characteristic of living matter, response to external stimuli? How can any living cell be acted upon by stimuli and yet not react to them? There is not a single observation to show that any germ cell, or its germ plasm, is in any way guarded or protected from external stimuli, either by the structure of its cell wall or peripheral cytoplasm, or by the nature of the living tissue that encloses it. And whatever affects the cell body must indirectly affect the chromosomes, because of the physiological connection of the two.

From such considerations it would seem practically certain that the energies of the chromosomes are to some extent respondent to environmental stimuli. And since observation shows that living matter responds differently, if not always according to the nature of the stimulus at least to its degree, it would follow that change in the nature or degree of the environmental agencies would indirectly engender change in the activities of the germ plasm. Not to admit this would be to deny to the germ plasm, without empirical reason, properties proven for all other living substances.

This thought had long ago been expressed clearly, though from a different line of reasoning, by Spencer (1865). We may state it in another way. Tissue cells are granted by experimental physiologists the ability of different response, or different intensity of response, to stimuli of different kind or degree. But a tissue cell is a lineal descendant of a germ cell, and receives germ plasm from the latter. Now

since the germ plasm has been transmitted continuously to the tissue cell, must not the energies of the germ plasms of the two be alike at least in their general response activity? Again, a Protozoan may be considered as a cell not exactly correspondent to a germ cell of a Metazoan, but as something more, as a unit with properties of both a germ cell and a tissue cell, for its cytoplasmic differentiations (cilia, contractile vacuoles, cytopharynx, etc.) are comparable to the soma of a Metazoan. In the case of the Protozoan *Paramoecium* Calkins (1904) has shown that the reproductive activity is increased or diminished according to the amount and kind of food stimuli. Here then a Protozoan has its reproductive activities, therefore the energies of its germ plasm, profoundly influenced by environmental changes; and it is primarily what we may term the germ cell constituent of the Protozoan that becomes influenced, that part which has to do with reproduction of the individual. Weismann considered the Protozoan exactly comparable, in the sense of strict continuity of reproduction, to the germ cell of a Metazoan, and yet failed to note that a Protozoan can be influenced by environmental change.

Accordingly, an environmental change may be capable of inducing change in the energies of the germ plasm. The expression of the energies of this substance, as viewed in temporal succession, constitutes heredity. Therefore the process of heredity may become modified by a change in the environmental conditions of the germ plasm. And since we defined variation as a modification of heredity, a variation could be produced by external influences acting upon the germ plasm, understanding by external influences influences of the tissue cells upon the germ cells, or, in case the germ cells are not enclosed, influences of the non-living environment.

All this reasoning seems to be quite different from that of

Lamarck (1809), who ascribed variation to modifications set up by environmental agencies in the "nervous fluid." But the end result of both arguments is very similar, and is Lamarckian in principle: variations may be induced by environmental changes. This is a permissible conclusion, for it is in accord with all we know of the physiology of the germ cells. An opposite view can be maintained only when there is evidence to show that the germ cells are physiologically entirely independent of the body cells, the germ plasm of the cytoplasm, and both of the environment.

Parenthetically attention may be drawn at this place to the recent change in ideas concerning the nature of response of organisms to stimuli, what previously had been named irritability. The theory of tropisms has long occupied a high place as an interpretation of the phenomena. Jennings (1904) names as the essential points "in the prevailing theory of tropism: (1) That orientation is the primary factor in determining the movements of organisms into or out of certain regions, or their collection in or avoidance of certain regions; (2) that the action of the stimulus is directly upon the motor organs, of that part of the organisms upon which the stimulus impinges, thus giving rise to changes in the state of contraction, which produces orientation." The tropism theory practically regards the organism as passively actuated by external influences, and is most radically mechanical in interpretation. Jennings combats it on the basis of a long series of beautifully analyzed reactions in different organisms, and since his observations are more extensive than those of anyone else, and so worthy of the fullest consideration, we may quote his final thoughts. "The general conclusion is drawn that the theory of tropisms does not go far in helping us to understand the behavior of the lower organisms; on the

contrary their reactions, when accurately studied, are as a rule, inconsistent with its fundamental assumptions. The responses to stimuli are usually reactions of the organisms as wholes, brought about by some physiological change produced by the stimulus; they cannot, on account of the way in which they take place, be interpreted as due to the direct effect of the stimuli on the motor organs acting more or less independently. The organism reacts as a unit, not as the sum of a number of independently reacting organs." This view seems to me far better founded than the tropism theory. And it is of importance in our present connection in showing the probability that the germ plasm acts in conjunction with the other living material, and does not pursue a wholly independent course.

How the environmental change induces change in the energies of the chromosomes we cannot tell. Surely the energy of the stimulus becomes translated into a very different one within the germ cell. A dead fluid substance is introduced, *e. g.*, and the germ plasm makes living material of it; the food substance may enter simply by way of osmosis, but the germ plasm elaborates it. In other words, the nature of the response is quite different from that of the stimulus. Therefore we must conceive of the process as an interaction between environmental and chromosomal energies, in which the initiative stimulus is change in the environment.

But it may be asked, even though this be true, may not the germ plasm have the power of automatically producing variations independent of environmental influence? This is the very question we have had in mind all along, because it is a matter of particular interest to the phylogenist. If this idea were true, then we should have to conclude that all phylogenies have been definitely predestined from the start by the nature of the germ plasm, that all races as we

know them to-day should be the outcome of certain prophetic variation tendencies of the ancestral germ plasm. The significance to the phylogenist is just this: is descent with modification the expression of a plan of development inherent in an early germ plasm? Or is it the expression of germ plasm energies acting in combination with influences of the environment? In the former event the phylogenist should not have to consider environmental action, the whole problem would be one of germ plasm energies; in the latter, he would find an analysis of environmental conditions essential to the analysis of racial descent.

It will be recalled that Nägeli (1884) in his theory of a hereditary idioplasm considered this substance to be continuous from generation to generation, as the basis and bearer of hereditary qualities. In the modification of the race he supposed there to be a tendency towards greater progression or perfection, which is to his mind the action of external and internal stimuli upon the idioplasm; no amount of purely external causes can produce changes that become hereditary, but only when acting in conjunction with internal causes. This he conceived to be the response of the energies of the idioplasm to external stimuli, produced when the latter are sufficient to modify the molecular arrangement of the idioplasm. De Vries has thought of the process taking place in premutation in much the same way. Thus Nägeli recognized, as Spencer before him, that heredity may be modified by external stimuli that change the hereditary substance.

Weismann at first assumed the germ plasm to be undisturbed by any factors that affect the soma, and so argued against the possibility of inheritance of characters acquired by the body of the individual. But enlarging the hypothesis first mentioned by Roux, that there exists a struggle for existence between the parts of the organism,

he now ascribes the origin of variations to germinal selection.

His idea is as follows (1902). The determinants are considered to be in a state of correlated equilibration; these determinants are hypothetical components of the germ plasm, each supposed to determine the development of one particular part of the embryo. They must be nourished, and the source of their food is from without; their rate of growth will depend upon the amount of nourishment, and since some determinants will obtain more food than others, the former will grow faster. "The rate of growth depends not only on the amount of nourishment; for in the same nutritive food one cell grows rapidly, the other slowly; it depends much more and to great part on the cell's power of assimilation. Thus the power of assimilation, affinity for nourishment, would also be different according to their constitution, and a weaker determinant would remain smaller, even with equal amount of nourishment, than a stronger one. The individual, hereditary variability appears to me to depend in the last instance upon the unequal nourishing of determinants, caused by accidents in the amount of nourishment." This is germinal selection in contrast to Darwin's personal selection. These two processes have no immediate connection, "and just in this lies the high value of this play of energies in the germ plasm, that it creates variations wholly independent of the relations of the organism to the environment. Personal selection of course takes hold in many cases, but even then it cannot directly cause the rising or falling of the several determinants, for these are processes that are wholly removed from personal selection. . . . Personal selection operates by removing unfavorably varying individuals from the genealogical tree of the species, but thereby removes at the same time unfavorably varying determinants

also, and so stops for all time their varying" (1902, p. 134, vol. 1). So both Nägeli and Weismann virtually admit that the first stimulus to variation is to be sought in action of the environment. This is of course the view also of the neo-Lamarckian school, and has been well expressed by Cope (1894) and O. Hertwig (1898).

Our conclusion is that variation, progressive or regressive, and also mutation, in fact any inherited modification of the race, is instituted by stimulus of the environment, by a change not appearing first within the germ plasm. This is shown by the fact that the germ plasm is not isolated anatomically or physiologically, and that the germ cells, so far as is known, possess the same property of response as do other cells or whole individuals. Under these conditions it is unthinkable that the germ plasm should not become influenced by external stimuli; and on the other hand there is no evidence of any kind that the germ plasm can within itself produce variation, for that would be virtually equivalent to an act of spontaneous generation. A rearrangement of particles of the germ plasm, thus new association of them, has been held by de Vries the cause of mutation; but then what causes this rearrangement? Since a stimulus from the environment can bring out a response from the germ plasm; and since a stimulus different from the usual one could induce an unusual response; then if the stimulus be of such a kind as to induce a marked change in the response, to modify the energies of the germ plasm, its result might well become inherited.

Thus we must decide that inherited variation results from the interaction of external influences and energies of the chromosomes. And there is no evidence at all of the presence of any perfecting principle in the sense of Nägeli, prophetically determining descent with modification.

One other possible source of variation suggests itself, that

induced by the cross-breeding of individuals of not exactly the same line of descent. Here there is an intermixture of two different germ plasms, whose properties differ as much as do the individuals that contain them. It is inconceivable in such a case, and contrary to observation, that any hybrid of such a cross in the immediate generation should be exactly like both parents. Thus Linnaeus, who held the idea of the separate creation of genera and species, allowed that new forms might be produced by the crossing of distinct species. Two kinds of hybrid conditions are now known, though these probably do not include all that occur in Nature, and the two may be associated in the same individual. One kind is that distinguished and described by Mendel (1865). It is, according to the experiments of de Vries, characteristic of crosses of retrogressive and degressive mutants, accordingly of what de Vries calls varieties. Its chief characteristic is the splitting or sorting of the parental characters among the different hybrid offspring, and its end result, after a sufficient number of generations where the hybrids are continuously cross-bred, is that one-half of the hybrids are like one parent, and one-half like the other. Thus the final result of Mendelian hybridization is the complete restitution of the parental forms. Obviously such hybridization cannot lead to the formation of new species. The second kind was first characterized by Macfarlane (1892) and named by him the unisexual. The significance of this kind has only recently been fully interpreted, namely by de Vries. The latter finds that unisexual hybrids are characteristic of a cross between a progressive mutant and an individual that is not a progressive mutant. A progressive mutant is an individual possessing a quality new to the race. It is a cross between two individuals that are essentially alike, save that one has a character not possessed by the other; because only one

of the parents has this character the cross is termed unisexual.* In such crosses de Vries maintains that this unimpaired character is transmitted to all of the offspring. By this kind of hybridization, accordingly, a new character would be promulgated in the race, hence a mutation be transmitted by crossing.

Yet, clearly hybridization has not produced this new character, but serves only to promulgate and make it evident. For in the words of de Vries (1903): "Each progressive mutation is in reality a double process and consists in the formation of a new, inner anlage and in its becoming active. Both processes might sometimes happen simultaneously, but they need not do so. Therefore it is desirable to denote them with separate names, and we call the inner process premutation, and the outer, perceptible, on the other hand, mutation in the proper sense. On this account premutation is of hypothetical, and mutation of empirical nature." In other places de Vries shows that visible mutations are rare, varying from 1:100 to 1:1000 or less. He points out that the chance of the meeting together of two mutating germ cells is minimal, and that in most cases a mutant would cross with a non-mutant. "There must clearly be just as many such bastards in each generation, as there are mutated sexual cells. Each visible mutation in our example must then have arisen as a bastard between a mutated and a non-mutated sex cell, when we disregard the rare meeting of two mutated cells" (vol. 2, p. 504). There is here no engendering of a mutation, but simply its transmission. De Vries reasons quite correctly for a premutation period when a change takes place in the germ plasm before change becomes visible in the descendants. That period of premutation may be hypothetical, in-

* It is unfortunate that de Vries adapted Macfarlane's term; "uniparental" would have been more apt.

asmuch as it has not yet been susceptible of observation; but it is nevertheless logically certain, and may yet prove empirically determinable.

It follows, accordingly, that in neither of the known kinds of bastardization, the Mendelian or the unisexual, is there any evidence that variations or mutations are produced by these processes. Parental qualities are transmitted according to more or less definite laws, but no new ones are produced.

The conclusion that hereditary variations are due in the first instance to external stimuli inducing change in the germ plasm must apply also to mutations. For if this be not so, we come up against the physiological obstacle of a change occurring automatically. If, according to the concept of de Vries, who does not attempt to solve the first origin of mutations, a mutation is due to a rearrangement of the physical units of the organism, it is a question of what produces this rearrangement. It is hardly conceivable that these structural units should group themselves differently from the normal condition, if all the stimuli that affect them remain unchanged. These hypothetical units are surely components of the germ plasm, and the latter acts and reacts like other living substance; there is no evidence that they and it can produce spontaneously but rather that they change their action only under change of stimuli. And in this regard it is significant that the very plant species, *Oenothera lamarckiana*, on which de Vries made his experiments and founded his conclusions, had been introduced to Europe from its original home in America: mutations in a species that had undergone great change of environment.

If the foregoing conclusions are justified it is evident that there is an inheritance of acquired characters. Indeed, the very postulation of the question "are acquired characters

inherited?" is absurd. It should read rather, "what kinds of acquired characters become inherited?" In the facts of transmutation of species, in every step of the changes undergone by them in the course of time, we have an indubitable case of the hereditary transmission of characters acquired in the history of the race. For each step in transmutation is the inheritance of a new character that has become acquired. It makes no difference at what period of the life of the individual an acquisition first appears, at what age the individual becomes affected; there is no justification in calling acquired only such characters as appear late in life. This does not mean that every new character acquired by any individual becomes inherited; far from it, as many observations show. But it does signify that each racial change is due to the inheritance of a character acquired by individuals. So the most recent criticism of the Lamarckian view is not pertinent, that of Morgan (1903), because it neglects the patent phenomenon of inherited acquisition by every race. Morgan argues that because some effects of use and disuse do not become inherited, therefore inheritance of acquired characters is "not proven." What is any racial change but an inherited acquired character?

Only a few thinkers seem to have grasped this question rightly, Lamarck, Spencer, Cope, Eimer, and Hyatt. Cope (1896) has summed up the matter clearly in the simple statement: "That all characters now congenital have been at some period or another acquired." In short, any individual of a race that has undergone modification is an example of the inheritance of acquired characters. This does not by any means imply that all characters that an individual acquires are bound to become inherited. Therefore the action of the environment is found to be not only plausible but probable. The mistake made by some of the

Lamarckians is in supposing that the greater number of acquired characters become inherited, though Lamarck himself did not make this error.

On this matter de Vries has to say (1901): "This depends to great extent upon a word play. Just according as one chooses his definition for acquired characters, he regards them as hereditary or not. . . . The mutations clearly fall outside the concept of acquired characters. In this matter doubt seems to me impossible. They arise suddenly, immediately and without reference to the environment; they are germinal variations in the purest sense of the word." According to him the individual variations alone represent acquired characters. "The mutations are hereditary and usually constant from the instant of their appearance. The variations or departures from the mean of the type are hereditary in wholly different manner. The children depart on the average less from the type than do the parents; on the other hand some tend to depart more strongly, and one can increase this departure through their descendants. . . . The individual departures from the mean species characters . . . depend in their amount, so far as the small experience reaches, upon the environmental media; but the latter can increase their influence through several generations." Here, however, de Vries himself makes a word play: acquired characters, according to him, are those only which do not arise suddenly, *i. e.*, individual variations and not mutations. But according to all essential ideas of his mutation theory the mutations are much more distinctly, even solely, steps in the formation of races, and a step in racial progress is surely nothing less than an acquisition. In showing that mutations become inherited he has really demonstrated an inheritance of acquisitions; and he even goes further, and admits that individual variations may become inherited. Again de Vries

has not in any way shown that the changes in the premutation period are spontaneous changes of the germ plasm.

All inherited differences, both variations and mutations, must have their inception in changes of the activities of the germ plasm, more precisely, of the chromosomes. But such change in activities can be produced only by change in the stimuli affecting the chromosomes, and the change in such stimuli is ultimately referable to changes in the environment outside of the organism. This idea is the one in fullest harmony with what we know of the process of heredity, of the interdependence of germ cells and body cells, and of the response of living substance to change in stimuli. A mutation would become inherited because it may be a profounder change than an individual variation, but it may differ from the latter rather in degree than in kind; only profound change of germ plasm response could become inherited. That would be the reason why slight characters acquired by an individual do not become inherited.

CHAPTER VI

THE TRANSMUTATION OF SPECIES

THOUGH the idea of the changeability of species has come up in many different minds at different times, and thus in its inception is a very ancient one, yet to Lamarck more than to any other single man belongs the credit of being its founder. More than any one of his predecessors he thought out a far-reaching theory, based upon geological changes of the globe as well as upon biological similarities, a theory connecting for the first time environmental relation with physiological correlation. Not to the first statement of the idea, but to its first full exposition must the credit be given, and in the long run the latter is always the adjudgment of Science. A few years before him Erasmus Darwin expressed the same thought, but the short chapter in his "Zoonomia" bears no comparison with the detailed reflections of the "Philosophie Zoologique." Lamarck found no immediate applause, not because he was lacking in clearness, logic and fullness of comparison, but because he was opposed by the scientific mentor of that day, the great naturalist and statesman, Cuvier. Darwin's work appeared in a time when men were more independent in thought, and more desirous of new generalizations, and accordingly from the start exerted an influence. Fairness to Lamarck cannot in any way depreciate our admiration for Darwin.

That there is change or transmutation of species, and that all the known forms of life are not results of separate

acts of creation, is no longer a hypothesis but as much a fact as other phenomena to which that word applies. The theory has never been disproved since the time of its comprehensive expression by Lamarck. Not a single living phenomenon has been shown to contradict it, and the criticism has been all upon negative evidence. The opponents to it have long urged the objection that no species have been observed in the process of transmutation; and the upholders of the theory have for the most part contented themselves with the answer that the process must be generally so slow as not to be perceptible within the compass of a human life-time, or even not of many centuries. But there are actual cases where the transmutation of species has been observed. The greater body of such evidence is furnished by the domestic and cultivated races of plants and animals, so that one might well say that any gardener's catalogue or breeder's guide is a tabulation of such cases. On such objects Darwin based many of his conclusions. These new forms of the gardener and the breeder may be considered variants or mutants or species; it is not here a question of just how they are to be classed. The point is that species have frequently been changed into forms hitherto unknown, unlike organisms that lived before them, and this not by any process of independent creation. Schrankewitsch (1877) was able to transform the Crustacean *Artemia* into another genus, *Branchinecta*, within a few generations simply by a change in the salinity of the water. The mutants of the primrose, *Oenothera*, described so fully by de Vries (1901), occurred as mutants while wild in the fields, and were simply brought into greenhouses for purposes of cross-breeding. These are the cases that are best known. Equally decisive to the mind of the naturalist is the great mass of data concerning geographical subspecies, to which we shall return, of intergrading races that cannot

be at all understood on the idea of any special creation hypothesis. For these reasons there is no longer any necessity to bring proofs in substantiation of species change.

This transmutation is of course the very keystone of all study of racial descent, and without it there could be no phylogeny.

The first formed life must have been homogeneous, structurally if not chemically. A general evidence of this is that the number of kinds of specializations decreases with lower relative phylogenetic rank. Now, are all known forms of life referable to a single ancestral group, or to several or many? This is the question of monophyletic (monogenistic) or polyphyletic (polygenistic) origin of groups.

Haeckel (1866) considers it most probable that there were in the beginning many acts of spontaneous generation; that of these earliest, homogeneous organisms only a small number persisted to produce more complicated organisms; and that from these few all the known organisms have been derived. This is essentially a monophyletic condition, one which Lamarck also had urged, and so Haeckel construed it, even though both postulated numerous primal acts of spontaneous generation. It is monophyletic because all known organisms, living and fossil, are referred to a single ancestral group.

Polyphyletic origin, as originally defined, meant that each known species had its peculiar ancestor like to itself; that as many species were present at the beginning, whether created or formed by spontaneous generation, as are now known. This is untenable in the light of the facts of transmutation. A modification of this view is that of Erlsberg (1874) and Nägeli (1884). These writers mention as one of the arguments against monophyly, that it implies that all living forms must be of the same age if they had a common ancestor, and so should be of approximately the

same degree of complexity, whereas at the same time exist together the most complex forms and the very simple. But this objection is strong only with the acceptance of the hypothesis of Nägeli, to the effect that his postulated hereditary idioplasm is actuated by a continuous perfecting principle, leading towards greater structural and physiological advancement. Were this hypothesis correct, then of course all organisms of the same age might be of the same relative degree of complexity. But the phenomena of heredity, as we have seen, give no evidence that the germ plasm is actuated by any such tendency; rather that its tendency is not to change except under environmental stimulation. So this objection to monophyletic descent has no good foundation.

The Nägelian view of the origin of species offers still another side. That is, that the idioplasm is continuous through the whole race, and in each geological epoch gives rise to new species, like an enormous mycelium extending through all time and forming periodically new growths. This ancestral idioplasm was postulated to consist of the simplest organic units, micellae, and, to continue our figure of speech, these would compose the stem of the mycelium; while the idioplasm in the branches would be much more complex. Therefore, from our standpoint that the most original life must have been homogeneous in structure and that no beings of such a nature are known in recent times, we must take a stand opposite the Nägelian, at least in so far as it necessitates the continuance of such a simple living material into recent times. Nägeli's hypothesis seems to be wholly without observational foundation.

We may conclude as the most reasonable position and the one most in accord with all general evidence, circumstantial and indirect though it be, that none of the organisms which offer appreciable structural specializations are of

an equivalent scale with the first formed organisms. All organisms of any degree of complexity have probably arisen through transmutation, and spontaneous generation has probably originated only much simpler beings. All known organisms do exhibit differentiation, there is not known a single homogeneous one. Likewise it is probable that all known organisms are monophyletic. Whether they are all derivable from a single ancestral individual, or from a few such, or from a group of them, we cannot decide; and one of the problems in phylogeny is the determination of this very question. Because of the degree of probability of monophyletic descent, this idea may well be employed as a working hypothesis. On this assumption the field for comparison is greatest, since all organisms may be treated together; to assume polyphyletic origin would be to postulate that certain lines of descent, certain phyla, could not be compared in that they had separate origin. So no more could the four great types of Cuvier and von Baer be compared. There is no good reason to assume such separateness of origin. In this connection it may be recalled that no known organisms are more dissimilar than the Vertebrates and the Flowering Plants. But the ancestry of both points towards a common origin, towards unicellular organisms more or less like the Flagellates, which appear to share the characters of both animals and plants. There is much good evidence that this or some related group of the Protista approaches closely in its characters to the ancestral group of all higher organisms. Whether the Protista themselves are polyphyletic or monophyletic remains to be determined. But it is a fairly well justified hypothesis that the known Metaphyta and Metazoa have had one common origin, so that all their component branches may be compared.

The objects that offer material for phylogenetic study are

the known organisms, those living now or those known as fossils. Hypothetically assumed ancestors are not such objects, and therefore the earliest conceivable forms of life, so long as they remain removed from observation, should not be seriously considered by the phylogenist. Ancestral or connectant forms may be deduced from comparisons of known organisms, but they constitute simply theoretical inferences. The hypothetical ancestor should not be granted the respect so often accorded him by over-zealous advocates. From the casual inspection of certain writings, and most unfortunately those intended for beginners, one might infer that the *Moneron*, the *Gastraea*, the *Trochozoon*, and the *Bathybius* were more important, if not more real, than the living animals around us.

A question of very considerable importance is that as to whether transmutation of species is definitely directed. We have seen that there is no reason to believe with Nägeli in any internal perfecting principle. Yet it is clear that development has in certain cases appeared to proceed in definite paths, and not to have been erratic. So Cope expresses himself (1896): "It has been proved, as it appears to me, that the variation which has resulted in evolution has not been multifarious or promiscuous, but in definite directions. It has been shown that phylogeny exhibits a progressive advance along certain main lines, instead of having been indefinite and multifarious in direction." This is seen in the case of the great specialization of the tarso-metatarsal joint in Birds: no such complete concentration and ankylosis of corresponding bones occurs in any of the Reptiles, yet all modern Birds possess it. Similar are the cases of the formation of trituberculate teeth in Mammals, of the concentration and fusion of metameres in the head region of the higher Vertebrates and Insects, of the progressively increasing complexity of the heart in Vertebrates, that of the

spinnerets in Spiders, etc. The modification of the feet of Horses is a favorite illustration of this.

All such phenomena appear to be examples of definitely directed development, of successive steps leading towards a certain end. The phylogeny of almost all organisms, when understood to some degree of completeness, seems to furnish proof of this view, in that there is a more or less straight progression towards certain racial stages. When we examine such cases in detail we find that usually such definite direction is limited to only certain parts of the organism. Thus in the case of the series of Mammalia definite appears the progression of the teeth and the structure of the hands and feet, but, as Osborn (1902) has shown, these are not correlated; and much less definite is modification of tails and horns. This shows clearly that the organism as a whole need not be progressing in a particular direction, but only certain of its characters. Unless evolution of particular parts were in particular directions for considerable periods of time, either progressively or regressively, there could not have occurred transmutation to the extent that we know it; but all structures must have remained in approximately their ancestral condition, and should show differences from each other perhaps not much greater than the extremes of the variation series in a comprehensive species. For whether the steps of evolution be gradual or discontinuous, no single step is known to be so great as that from a Fish to a Batrachian, or from a Flat-worm to an Insect. Hence there must be several or numerous advances, their number in indirect ratio to their degree, to produce a descendant markedly different from the ancestor; and, further, they must all be advances in the same general direction, for otherwise they would negative one another. From this simple consideration it becomes plain that all evolution leading to considerable departures in the de-

scendants of the race is definitely directed, *i. e.*, consists of a series of changes more or less similar in kind. If a race advances progressively up to a certain point of time and then regressively, as has been the history of so many parasites, it obviously exhibits two contrasted paths of definitely directed transmutation, with an interruption between them. The Nägelian perfecting principle takes no count of regressive evolution.

All transmutation of any considerable extent must then be definitely directed evolution. But the direction may change its course at intervals, and descent may be graphically represented by an arborization, and not by divergent straight lines. Such deviations in no way contradict the idea of definite direction, if we think of the latter as not a straight line but rather an irregularly angular one. Further, each character of the race seems to proceed along a more or less independent path of its own, beyond certain few characters that may always develop in correlation. Yet it does not at all follow that such definiteness has been the outcome of predestined tendencies in the ancestral germ plasm; there is no evidence for this. The end results have probably been attained by the successive reactions of the germ plasm to changed stimuli, and were not planned out in the original germ plasm. A change of environmental stimuli in one general direction could well account for definitely directed evolution. Herein lies the great point of difference between the development of the individual and of the race: the former is predetermined by the character of the germ plasm of the fertilized egg, the latter by germ plasm energies reacting to successive external stimuli. How long transmutation would proceed along one definite road without deviation, would be to some degree dependent upon the path of environmental influence, but by no means in direct proportion to it.

Another point remains for consideration: is evolution continuous or discontinuous? Darwin held that it proceeds for the most part gradually and by minute accumulations, but admitted that it may occasionally go on discontinuously, by sports. Wallace and Weismann have argued for gradual change, without distinctly making Darwin's admission. Most of the neo-Lamarckian argument has been to the same effect. This view sums itself in the old Linnaean aphorism, *Natura non facit saltum*. On the other hand, Dollo (1893) and Scott (1894) first, from paleontological evidence, then Bateson (1894) from the statistical study of variation, most recently de Vries (1901) from the study of the transmission of characters in hybridization, have maintained the occurrence of mutations or discontinuous variations, and have argued that transmutation is due to them. The evidence of variation from statistical studies and from experimental cross-breeding is of course more accurate and therefore more decisive than the more indirect paleontological inferences. De Vries gives the following definition of his mutation theory: "The theory of mutation I call the statement, that the characters of the organism are composed of units sharply defined from each other. These units can be joined in groups, and in related species the same units and groups are repeated. Graduations such as those which the external forms of plants and animals so frequently offer, exist between these units just as little as between chemical molecules." He has described the sudden appearance of forms differing from the parent stock in characters evidently not possessed by the latter; and this is accordant with his working hypothesis that the organism is a complex of characters that do not intergrade.

However, the important result remains that transmutation may be in some cases discontinuous, by mutations. There is apparently no definite experimental proof that

transmutation may proceed continuously in some cases also, that is, by individual variations, though even de Vries admits that continuous variations may be to slight extent cumulatively increased through successive generations. That there is the possibility of continuous evolution we shall now attempt to show.

What has long interested students of evolution is the interpretation of geographical races, or subspecies, of the larger plastic and variform species. These have always been the *bêtes noires* of the systematists who desired rigid definitions of their species. An excellent case in point that has long interested me is that of the races of the American Song sparrow, *Melospiza cinerea* (Wils.). The particular races as they have been recently redefined by Ridgway, and their ranges, are as follows:

Melodia cinerea melodia—Atlantic watershed.

M. C. montana—Rocky Mountain plateau.

M. c. cooperi—Coast district of southern California to San Quentin Bay, Lower California.

M. c. clementae—San Clemente, San Miguel, and Santa Rosa Islands, California.

M. c. graminea—Santa Barbara and Santa Cruz Islands, California.

M. c. pusillula—Salt marshes of San Francisco Bay.

M. c. mexicana—Southern portion of the Mexican plateau.

M. c. adusta—Southwestern edge of the same plateau.

M. c. goldmani—Pine belt, mountains of Durango, Mexico.

M. c. heermanni—Lower Sacramento and San Joaquin valleys, California.

M. c. samuelis—Coast district of middle California.

M. c. cleonensis—Coast district of northern California.

M. c. fallax—Lower Sonoran district of southwestern

Arizona, southern Nevada, southeastern California, north-eastern Lower California, Sonora.

M. c. rivularis—Southern Lower California.

M. c. morphna—Oregon to southern Alaska.

M. c. rufina—Sitkan district of Alaska.

M. c. caurina—Coast of middle Alaska.

M. c. insignis—Kadiak island, and the opposite coast of the Alaskan peninsula.

M. c. kenaiensis—Coasts of Kenai peninsula, Alaska.

M. c. cinerea—Aleutian islands, east to the lower portion of the Alaskan peninsula.

Ridgway states the following in regard to the intergradations of these races (1901, pp. 350-352): "The type-species of this genus is a bird of very extensive geographic range, breeding throughout the temperate parts of the North American continent, including the plateau of Mexico. No other bird in the Nearctic Region has proven so sensitive to influences of physical environment, and as a result of this plasticity of organization it has become divided into a large number of geographic forms, some of extensive, others of very circumscribed range, the area of distribution in every case coinciding strictly with uniformity or continuity of physical conditions. Thus the form having the widest distribution is that inhabiting the Atlantic watershed, or the entire region from the wooded valleys of the Great Plains eastward, while those of most limited range belong to the Pacific slope, where the topographic and resultant climatic features are so varied and complicated. In California, for example, practically each distinct drainage area has its own peculiar form, one being strictly limited to the salt marshes fringing San Francisco Bay. From the last-mentioned point, inhabited by decidedly the smallest of all the subspecific forms, northward along the coast there is a gradual change, the size steadily increasing, the plumage

becoming first more rusty, then more sooty, and finally more grayish, until the extreme limit of variation is reached in the gigantic *M. c. cinerea* of the Shumagin and Aleutian Islands. . . . While intermediates connecting some of the forms have not actually been seen by me, there cannot be the slightest doubt as to their existence, their absence being due in every case to lack of specimens from intermediate localities. . . . Except in the case of a few, where wide deserts or other physical obstacles prevent continuous distributions, there cannot, however, be the slightest doubt that intermediates will be found when specimens are collected at the proper localities."

From Ridgway's descriptions and comparisons I have reconstructed the scheme presented upon the preceding page. The unbroken lines connect races between which he states he has found intermediates, and the dotted lines races between which intermediates are expected by him to occur. This chart shows only very roughly the approximate geographical position of the races, the area in the north-southerly direction being greatly foreshortened.

There are in this species two main lines of supposed intergrading forms: (1) *montana*, *morphna*, *rufina*, *caurina*, *kenaiensis*, *insignis*, *cinerea*; and (2) *montana*, *heermanni*, *samuelis*, *pusillula*, *cleonensis*. The most continuously progressive series of races, judging from the measurements given by Ridgway, seem to be: *rufina*, *caurina*, *kenaiensis*, *insignis*, *cinerea*. The two extreme races of this last series show marked differences, as shown in the following comparison:

M. c. rufina—Coloration sooty. Average measurements of the male: wing, 72.14 mm.; tail, 70.10 mm.; length of bill, 12.45 mm.; depth of bill, 7.11 mm.; length of middle toe, 17.53 mm.

M. c. cinerea—General color above gray, almost ash-gray. Average measurements of male: wing, 85.09 mm.; tail, 82.55 mm.; length of bill, 16.26 mm.; depth of bill, 8.38 mm.; length of middle toe, 20.07 mm.

It will be noted that this series from *rufina* through *caurina*, *kenaiensis*, and *insignis* to *cinerea* appears to be a perfectly gradual one, without break in characters of dimensions; and the respective geographical areas follow each other continuously also.

Here let us consider the significance of these subspecies of the Song sparrow. Are these subspecies or races variants or mutants? This question is a very important one, for there is much general, if not precise, evidence that certain species now recognizably distinct, *i. e.*, not intergrading, and even without overlapping areas of distribution, were once geographical races of one larger species. This is Darwin's interpretation of them, and a view that has been quite generally held by systematists. If there be an actual and complete intergradation of the individuals composing these races, then *ex definitione* they would be variants.

Now in the case of the Song sparrow some of these races do seem to perfectly intergrade. To be sure, large numbers of specimens of each have not yet been statistically studied. But so far as is at present known it seems to be a perfect intergradation, so that we will assume the condition to be such until the contrary is demonstrated. These are then, from the standpoint of their characters, variants and not mutants. The differences well seem to be such as would be dependent, further, upon differences in food, soil and climatic conditions. Then there is a second consideration. It appears to be the case that all the individuals in one geographical area are different from all the individuals in a contiguous area, and that intermediate individuals occur

only where the two areas overlap. There is, accordingly, geographical intergradation of the areas, and connecting character gradations coincide with continuously succeeding geographical areas. This speaks strongly against the inference that such races should be mutants. Because if they were mutants how could be explained the phenomenon that the succession of character differences coincides so exactly with geographical succession? For we could imagine mutants arising successively (1) at either one point in the geographic area of the species, or (2) separately and at different points. If they arose by the first method, why should the descendants of a particular mutant all move to one portion, and of another all to another portion of the area? Or if separate mutants appeared at different localities within the area of distribution, what would be the power of regulation to arrange their descendant mutants in a geographical sequence coinciding exactly with the degree of difference of their characters? It might be answered that natural selection could bring about such a distribution. But even were there a very active process of selection in operation, it would be exceedingly difficult to explain by it such geographical gradation of the races as are found in the Song sparrow. The point is just this: if these races be mutants, the mutation theory could not explain why geographical series should coincide with the sequence of character difference. No more can it account for the fact that where the geographical area is the most varied, there occur the greatest number of forms. In the area of *Melospiza cinerea cinerea*, the largest form, have never been found examples of *M. c. pusillula*, the smallest, nor has the former been found within the proper district of the latter; but only individuals of those races are found together whose areas overlap.

These races of the Song sparrow are then probably

variants and not mutants. And another point is to be noted. These variants probably breed true, else we could not understand why all those in a given area show the same characters and why there is no irregular intermingling. Whether they would continue to breed true if removed to different environmental conditions, remains to be tested; but this does not concern us at present.

This brings us logically to an important conclusion. If the extreme variants in the Song sparrow series should continue to increase their degree of variation cumulatively, as even de Vries admits it is possible for variants to do, while concurrently the connecting variants should become extinct, there would result geographically separated races that would no longer intergrade. In other words, from perfectly continuous variation distinct forms could arise. It is a matter of definition whether they be called at first different species or not. It is, however, quite possible that two such distinct races by separating geographically still more from each other should become still more distinct, particularly if cumulative variation goes on. Their differences could then no longer be regarded simply as ones of degree, and on any generally accepted definition of species they would have to be considered separate species. In this way new species could be formed from variants, therefore from gradual individual variation.

De Vries has shown that new species may appear suddenly, disconnectedly, as mutants. It is certainly a very alluring and genial hypothesis that such is the only mode of origin of species, but this has not yet been demonstrated, and the author of the mutation theory himself grants that mutation may not be the only mode of formation of new species. On the other hand, the study of intergrading geographical races, such as those of the Song sparrow, makes it probable that such races are sometimes variants and

not mutants, because this view alone explains satisfactorily their geographical gradations. And we have just seen that the extremes of such races may become so distinct that in the event of the extinction of intermediate forms they must be considered distinct. To adopt de Vries' definition of species, as forms possessing characters differing not in degree but in kind, would be to conclude that such disconnected variants would not be species. Yet these extreme variants seem to breed true within their respective habitats, which is a generally accepted criterion of species. And it is altogether possible, just as Darwin so lucidly reasoned, that in the course of time such extreme variants would come to differ in kind also. Therefore the mutation theory has not disproved the possibility of perfectly gradual transmutation of species, but has only shown that sometimes transmutation may not be a gradual process. My point of view in this matter is in essential agreement with that of Davenport (1903).

Because widely distributed species containing geographical races are so numerous, it is evident that in quite as many species, by the eliminating process of natural selection, intermediates between the several races have become extinct. This is notably the case with insular races of a species inhabiting also the neighboring continent, as particularly Wallace has shown. The mutation theory cannot explain why each of these islands should have developed its peculiar forms; why rather should not the same kind of mutant have appeared simultaneously upon all the islands, or different mutants upon the same island? In fact we should expect to find closely intergrading races only in comparatively young species, before natural selection has had time to bring about the elimination of some of them; and indeed degree of intergradation might become a test of the age of species. Accordingly, all those forms not connected with

others by intermediates, which present themselves to the student of racial descent, need not have originated as mutants, but some of them as variants; indeed there are reasons why many of them should have originated as variants.

It is well known that while many wide-ranging species exhibit geographical races, others do not, and it is customary to speak of the former as the more plastic. But this cannot be maintained *a priori*. One factor was pointed out by me in another place (1896), namely, that a species with a broad and diverse breeding area develops no geographical races when it has the habit of taking long annual migrations. This is seen clearly in Birds. And I explained it by the assumption that individuals do not become specially modified by the environmental conditions of their particular breeding areas, because in their Winter quarters, *i. e.*, at the opposite end of their migration route, they become subjected to a different environment. The effects of these two environments counterbalance each other, and the one does not permit special modification by the other. Thus our Barn swallow, with its broad breeding area from the Arctic Circle to Mexico and from the Atlantic to the Pacific, shows no geographical races at all, because it migrates as far south as Central and South America. While the Song sparrow, as we have seen, migrates very little when at all during the cold season (and then only from mountain sides into contiguous valleys), but has a great number of such races. On this account there is no reason to regard the Barn swallow as less plastic than the Song sparrow; we can only conclude that the former's two different environments prevent the formation of subspecies. But on the other hand there is the Short-eared Owl, which is nearly cosmopolitan in distribution, nowhere appears to have any extensive migration range, and yet has formed no geographical races at

all. The Song sparrow in this relation would be more plastic than the Short-eared Owl.

We are not able to state what determines plasticity and fixity of growth phenomena. Two kinds of individuals may be considered plastic, variants and mutants. There is some evidence to show that mutation plasticity is not omnipresent but periodical. Then there may be greater and lesser degree of plasticity in reaction to stimuli. Such are the cases of regeneration ("new growth," Darwin, 1866) of lost or injured parts. The evidence shows that some forms are much more plastic in regeneration than others, as is shown in the excellent book by Morgan (1900) on this subject. Plants in general exhibit this power to greater degree than animals do, and among animals certain Hydroids and Planarians much more than other forms; even closely allied species may show marked differences in regenerative power. It does not seem to be the case that power of regeneration decreases at equal rate with increase of structural complexity, but rather that other influences are concerned that we do not understand.* Yet *Hydra*, so conspicuous for its ability to regenerate lost parts, does not present geographical races, nor seems to be an extremely variable form. Plasticity in regeneration and plasticity in the formation of species appear then to be quite distinct states; and the whole problem of what constitutes plasticity in general remains a riddle, though its answer would be of great value to the phylogenist.

Species may arise continuously or discontinuously, and there is no reason to consider the second method as the sole one or even as the most usual. Mutants are distinct from the start from the parent forms; variants become distinct by the loss of intermediates. The new characters of

* It might be interesting to determine whether species in a state of mutation possess this power in a higher degree than others.

mutants while of kind and not degree are often very slight, and may be limited to a small part of one organ; other mutations may be of larger extent, as shown in the data collected by Darwin (1866) and Bateson (1894). Much more information is needed than we have at present, but what we have shows that where transmutation is discontinuous the degree of discontinuity is usually not great. From this conclusion it follows that the phylogenetic principle is correct, to anticipate connectant forms. There is little if any evidence for the view that a new form may be from the start entirely different from the parent. De Vries' analysis of his *Oenothera* bastards shows that a mutation generally concerns one character only and not all the characters. If this should be found true for all cases, then we should never anticipate the sudden appearance in transmutation of an organism with all its characters different from those of its parents.

Never have the factors of transmutation seemed more complex and problematical than just at the present time. In this little book there is not space for any adequate historical discussion of the various views, for that would require volumes. But attention may be drawn to the opinions of some of the main leaders in the discussion, on points which we have not yet considered by themselves.

In the first place the factors might be one of the following kinds: intrinsic, inherent in the properties of the living matter; extrinsic, lying without the organism; or some combination of these two.

That they are to greater extent extrinsic is the conclusion of Darwin (1859). He gives no explanation of the origin of variations, except in occasional passages accepting the Lamarckian factor of environmental influence; and interprets transmutation as a process carried out by selective agencies of the environment. Wallace (1881, 1903) is still

more consistent than Darwin in this respect. Only in his theory of pangenesis does Darwin (1866) try to analyze internal factors. This theory of personal selection is the only one that ascribes such dominant importance to extrinsic factors, and it leaves almost untouched the basic problem, that of the first origin of the differences.

Weismann (1902), while a strong follower of Darwin, has shifted the factors to the germ plasm, to a process of germinal selection taking place within the latter. And, in that he argues that the germ plasm is very considerably if not wholly removed from environmental influence, he considers the factors to be essentially intrinsic. But like Nägeli (1884), he admits some environmental influence upon the hereditary substance. De Vries (1901) expresses himself very strongly against selective creation in either the Darwinian or the Weismannian form; but since he ascribes mutations to changes in position of the germ plasm units, he is to be classed with Weismann as maintaining intrinsic factors, even though he has not expressed himself upon the initial cause of premutation.

Another interpretation argues for an interacting combination of external agencies and internal growth activities, holding that transmutation results from the effect of changes induced within the living material by external stimuli. This is the opinion of Lamarck (1809). He reasoned that environmental change, and use and disuse, bring about differences in the flow of the "nervous fluid" to the organ affected, and according to such difference the part increases or decreases in size, forms new growths, or loses old ones. This may seem to-day to be an exceedingly crude explanation. But we should be just, and recall that it was a distinct advance over the older views of a *vis essentialis* or an *anima*; and that Lamarck reasoned the organism to be not moulded by the environment as clay is by the hand, but

indirectly through the medium of the nervous system. With greater logic and the advantage of more facts, Spencer (1865) maintained the same conclusion. Cope (1894) went perhaps a little too far in ascribing too much to the environment and too little to the living energies themselves.

Of these three main interpretations we have accepted the one that the factors are neither purely extrinsic nor purely intrinsic, but a combination of the two. We are not to think of the environmental influence being direct in the modification it produces. The Lamarckians have gone too far in concluding that a mechanical modification can be directly inherited as such. Thus the enamel folds of a lower molar tooth are so apposed to those of the corresponding upper molar as to seem to have been formed by direct mechanical impact and strain. But it is probable the process is far less simple than this. Had a molar tooth once developed such a folded crown, whether by mechanical strain or otherwise, and had this been of such importance in the growth of the organism as to induce changes in the germ plasm energies, it would of course produce an inherited effect. But this effect need not show itself in the course of the next generation in the form of a ridged enamel crown; rather, for aught we know to the contrary, the effect might appear as a change in the form of the stomach or the jaw, or as a decrease in size of some other organ. There is no reason to conclude that this change would affect only those substances of the germ plasm which are, in the next generation, to give rise to a corresponding molar tooth. The former kind of argument is the erroneous part of the Lamarckian doctrine, not that part which ascribes all change in the race to an initial environmental stimulus.

Natural selection, as has been frequently pointed out of late, does not originate changes but merely selects be-

tween them. And it would seem to be a process of more import in destroying the bearer of disadvantageous variation than in preserving the carrier of the advantageous. It is best expressed by the term "elimination of the unfit." Undoubtedly natural selection, together with continuity of environmental change, has been of great influence in determining the definite direction of transmutation.

CHAPTER VII

PARALLELISM OF THE ONTOGENY AND THE PHYLOGENY

AN exceedingly fertile working hypothesis in phylogeny has been the view of the correspondence of the stages in the development of the individual with the steps in the transmutation of the race. The stages in the individual's embryogeny from the egg to the adult state constitute what Fritz Müller (1864) called the ontogeny, and the succession of changes of the race, the phylogeny. So much importance has been ascribed to this hypothesis, that frequently the question has arisen as to whether the study of embryology is not of more value than comparative anatomy, in determining genetic relationships.

There is clearly a correspondence to some extent between the two processes, for in both there is progression; in the words of von Baer (1828), each is an advance from the more general to the more special.

But there is stringent necessity to attempt to decide of what nature and degree this correspondence is, and on what it depends. For the decision has immediate practical bearing on the matter of how far the phylogeny may be correctly ascertained from an analysis of the ontogeny. Do the successive embryonic stages of the individual recapitulate the history of the race? Or do they only parallelize it? Or has the supposed correspondence in reality no existence? These questions can most profitably be answered after a preliminary historical statement of the rise of the hypothesis, and the critical treatment which it has suffered.

The following review is far from complete, because almost all embryologists have expressed themselves upon the subject; yet it presents the main changes of thought.

A. HISTORICAL

This has been named by Hatschek the "morphogenetic theory," by Hyatt the "law of morphogenesis," by Haeckel the "biogenetic law," by Cope the "doctrine of parallelism," and by Morgan the "repetition theory." Sometimes it has been alluded to as the "law of von Baer," but incorrectly, for von Baer was its severest critic.

The idea of a correspondence between the ontogeny and phylogeny is a very old one, which has not yet been traced to any single originator. Von Baer, writing in 1828, speaks of "the accepted idea, that the embryo of the higher animals passes through the permanent forms of the lower. . . . This idea which was born in a time when, besides Malpighi and Wolff, no connected investigations had been undertaken upon the earlier periods of the embryology of any animal, and was especially carried out by a man who possessed perhaps the most knowledge upon the embryology of the higher organisms, could not help but arouse great support, because it was based upon a multitude of special proofs. . . . Some supporters were so zealous that they spoke no longer of similarity but of complete identity, and acted as though the correspondence were proven universally and in each particular. We read a short time ago, in a paper upon the blood circulation of the embryo, that the human embryo does not omit a single animal form." That must indeed have been the luscious Spring time of the theory! And Wolff, writing in 1759, makes practically the same statement in regard to this then prevalent view.

But von Baer himself strongly criticised the idea of recapitulation. He mentions as empirical objections to it:

(1) that no adult animal ever has a yolk sac, or (2) is surrounded by embryonic fluids; (3) that it is not the case that an embryo of a higher animal in each embryonic stage corresponds in every point with an adult of a lower species, or (4) that in the ontogeny of a lower form structural relations do not occur which are found in the adult of a higher; (5) that it is equally not the case that parts which are characteristic of only the highest forms appear latest in the ontogeny. Then von Baer formulated the following laws of the individual development (l. c. p. 224). "(1) That the general of a large animal group expresses itself earlier in the embryo than the special. (2) Out of the most general of the structural relations evolves the less general, and so forth until finally the most special appears. (3) Each embryo of a particular animal form instead of passing through the other particular forms, separates itself rather from them. (4) In reality accordingly the embryo of a higher animal form is never like to another animal form, but only to its embryo." Thus he reasoned that a Chick is exceedingly early a Vertebrate, and that embryos of Vertebrates recapitulate no known adult forms of Invertebrates.

Von Baer in 1816, as is not generally known, antedated Cuvier in the establishment of the "type theory"; this is explained in the preface of the former's "*Entwicklungsgeschichte*" of 1828. So von Baer from the embryological side, and independently Cuvier (1829) from the standpoint of comparative anatomy, evolved the idea that all animal species are modifications of four main "types" or "*embrâchements*," that is, independent and equivalent "plans of structure" without intergradations. Louis Agassiz (1857) followed his teacher Cuvier in this type theory and in the hypothesis of periodic cataclysms, and, like him and von Baer, firmly maintained the idea of the fixity of species.

This explains the peculiar attitude of Agassiz towards the recapitulation hypothesis. He wrote (1857, p. 115): "It may, therefore, be considered as a general fact . . . that the phases of development of all living animals correspond to the order of succession of their extinct representatives in past geological times. As far as this goes, the oldest representatives of every class may then be considered as embryonic types of their respective orders or families among the living." And, on page 116: "These relations, now they are satisfactorily known, may also be considered as exemplifying, as it were, in the diversity of animals of an earlier period, the pattern upon which the phases of the development of other animals of a later period were to be established. They appear now, like a prophecy in those earlier times, of an order of things not possible with the earlier combinations then prevailing in the animal kingdom, but exhibiting in a later period, in a striking manner, the antecedent considerations of every step in the gradation of animals." This is his well-known concept of "prophetic types." Then again (p. 120): "No more complete evidence can be needed to show that there exists throughout the animal kingdom the closest correspondence between the gradation of their types and the embryonic changes their respective representatives exhibit throughout."

Thus Agassiz noted the correspondence between the ontogeny and the succession of ancestral forms, and between the gradations of structure within a type and the embryology of a member of the same type, but repudiated all thought of transmutation of species, and ascribed all to the "plan designed by an intelligent Creator."

Carl Vogt (1851) followed von Baer, and wrote (l. p. 17): "The embryo of the higher animal to be sure passes in its development through developmental movements which

are analogous to those of lower forms of the same type, but its transitory organization is never perfectly similar to that of lower animals in their mature condition. It is still more opposed to the truth when one asserts, founding upon inaccurate observations, that the higher animals pass in their development through conditions that are analogous to the adult animals of other fundamental types."

All the following writers upon the subject discard the von Baer-Cuvierian doctrine of distinct and independent types or moulds of structure; for this idea received its death blow in the idea of the transmutation of species.

The man who accomplished this great revolution of thought, who forced it upon men's convictions as Lamarck could not, was of course Charles Darwin. He has to say upon the subject at issue (1886, p. 395): "It is highly probable that with many animals the embryonic or larval stages show us, more or less completely, the condition of the progenitor of the whole group in its adult state. . . . In two or more groups of animals, however much they may differ from each other in structure and habits in their adult condition, if they pass through closely similar embryonic stages, we may feel assured that they all are descended from one parent-form, and are therefore closely related."

The work which more than any other has stimulated interest in the discussion of ontogeny and phylogeny is the little but genial and fruitful book of Fritz Müller, "Für Darwin," of 1864, a work deeply influenced by the "Origin of Species." And he did his work in the tropics of the Western Hemisphere, as Wallace worked and thought in the jungles of the Eastern. Müller writes: "The historical record (of the development of the ancestors) contained in the development (of the individuals) becomes gradually wiped out, in that the embryology takes an always more direct path from the egg to the adult animal, and

it becomes frequently falsified through the struggle for existence that the free-living larvae have to meet. The genealogy of the species (phylogenesis) becomes the more fully retained in its embryology (ontogenesis) the longer is the line of immature conditions, which the species traverses at equal pace, and the more accurately, the less the mode of life of the young differs from that of the adults, and the less the peculiarities of the several immature conditions may be conceived as pushed back from later into earlier life periods, or as independently acquired." Müller's thought is that the embryo or larva of a higher form is similar to the adult stage of a lower form of the same line of descent, provided secondary modifications, attributable to changed conditions of life, have not intervened.

Herbert Spencer (1865, 1 p. 366) concluded: "The resemblances which hold together great groups of embryos in their early stages, and which hold together smaller and smaller groups in their later and later stages, are not special or exact, but general or approximate; and in some cases, the conformity to this general law is very imperfect. . . . Hence, remembering the perpetual intrusions of organisms on one another's modes of life, often widely different; and remembering that these intrusions have been going on from the beginning; we shall be prepared to find that the general law of embryologic parallelism, is qualified by irregularities that are mostly small, in many cases considerable, and occasionally great."

Haeckel (1866) was one of the first to forcibly realize the truth that "the theory of descent alone enables us to explain the embryology of the organisms. . . . The ontogeny or development of the physiological individuals is inseparably and most intimately connected with the phylogeny or development of the genealogical stems (phyla). . . . How intimately these universally hang

together, how essentially they mutually necessitate and complement each other, how first out of the close fusion of the two the proper development of organisms in the full sense of the word may be constructed, is up to this time either not rightly valued by most biologists or even wholly overlooked." This is the key-note of the whole of the "Generelle Morphologie," the central point in his monograph of the Calcareous Sponges, and the idea guiding him in much of his later work. From his consistence and persistence in applying this idea, he has given a greater stimulus to the study of comparative embryology than anyone since the days of Wolff and von Baer.

Then Haeckel goes on to state that "ontogeny is nothing further than a short recapitulation of phylogeny," a decision in line with the earlier expression of the concept. And he attempts to explain this correspondence: "The parallelism between the phyletic (paleontological) and the biontic (individual) development is explained simply mechanically by the laws of heredity, and in particular by the laws of the simultaneous, the homotopic and the abbreviated heredity. All phenomena which accompany the individual development explain themselves simply, in so far as they are not immediate results of adaptation to new conditions of existence, from the paleontological development of the ancestors of the individual. The whole ontogeny is a short and rapid recapitulation of the long and slow phylogeny." Later, in his "Gastraea-Theorie," he formulated this more precisely, and distinguished in the ontogeny two processes: palingeny, the maintenance of the ancestral recapitulation; and cenogeny, the modification or falsification of it; both of which were recognized by Fritz Müller but not named by him. "Morphology which has conceived its purpose correctly will only then find the hidden path of phylogeny in the difficult region of ontogeny, when as far as possible it seeks out

the palingenetic processes, as far as possible eliminates the cenogenetic."

Hyatt in 1866 recognized the parallelism of the ontogeny with the "phylocycle," and in various memoirs upon fossil Cephalopods used this as an important guide in determining racial descent. This early paper was inaccessible to me, so I will quote his views as expressed in 1889, in the "Genesis of the Arietidae": "We have endeavored to demonstrate that a natural classification may be made by means of a system of analysis in which the individual is the unit of comparison, because its life in all its phases, morphological and physiological, healthy or pathological, embryo, larva, adolescent, adult, and old (ontogeny), correlates with the morphological and physiological history of the group to which it belongs (phylogeny)." And his doctrine of "acceleration in development" is: "All modifications and variations in progressive series tend to appear first in the adolescent or adult stages of growth, and then to be inherited in successive descendants at earlier and earlier stages according to the law of 'acceleration, until they either become embryonic or are crowded out of the organization, and replaced in the development by characteristics of later origin. . . . The law of acceleration in development seems, therefore, to express an invariable mode of action of heredity, in the earlier reproduction of hereditary characteristics of all kinds, and under all conditions. In progressive series it acts upon healthy characteristics, and appears to be an adaptation to favorable surroundings, and in retrogressive series upon pathological characteristics, and is probably an adaptation to unfavorable surroundings, usually leading to the extinction of the series or type."

Hatschek (1880) has as fully as any recent embryologist relied upon ontogeny in the study of relationships, and his ideas demand careful consideration on account of the value

of his memoirs. He introduces a new and important point of view: "We must consider it as a general law, derivable from the principle of causality, that with the phylogenetic modification of an animal form (individual cycle) never only the end stage becomes changed, but always the whole row from the egg cell to the end stage. Each modification of the end stage or the addition of new stages necessitates a change of the egg cell itself." This is to my mind one of the most important details in the whole criticism of the theory, and we will try to unravel its deep significance.

Later, in his "Lehrbuch" (1888), Hatschek develops his ideas more fully: "The phylogenetic modification accordingly takes place in most cases so, that an addition of new stages follows on the end of the ontogenetic row of forms. . . . When one premises (as Haeckel does) that the modifications, which the developed individual inherits directly through outer influences, become hereditary in its descendants, then the explanation shapes itself very simply. The new acquisitions of the adults bring about immediately a prolongation, in the single generation very insignificant, in the course of generations increasing, of the ontogenetic row of forms in the descendants. But when one holds fast to the view that only those newly occurring characters become inherited, which have arisen through variation of the reproductive cells (variation through the influence upon the organs of generation, according to Darwin), another explanation seems necessary. One must presuppose 'overstepping varieties.' With this name I would call such varieties, as consist in a prolongation of the ontogenetic row of forms. . . . Frequently the question has been broached, whether greater importance comes to comparative anatomy or to comparative embryology for the elucidation of the genealogical connection, *i. e.*, of phylogeny, of animals. The question is certainly a useless one,

for it is necessary to unite and to consider equally both methods of investigation." Hatschek goes further than Haeckel, in concluding that cenogenetic as well as palinogenetic characters are of value in the study of descent: "When we recognize a larval or embryonal form as characteristic for a whole animal group, we may not conclude therefrom that necessarily a similar phylogenetic stage is represented by the same. We are justified only in the conclusion that the ancestral form of this animal group had possessed that characteristic developmental stage. . . . But when a larval or embryonal form of higher animals shows a great agreement with the developed stage of lower animals, then we can conclude with great probability that the same corresponds to a similar ancestral form. . . . But this conclusion also cannot be drawn with perfect certainty. For a lower animal form can have proceeded from a higher by suppression of the end stages. . . . In the same way a secondary larval form could show agreement with a lower animal form, which had originated phylogenetically from a higher form through suppression of the end stages. . . . The results of comparative ontogeny have always only the worth of probability conclusions, just in the same degree as those of comparative anatomy. The relative certainty depends in both cases upon the number of the premises and upon the keenness of the argument."

Lang (1887) expresses one of the points made by Hatschek in somewhat different phrase: "If according to the descent theory the adults differ, in the great majority of cases, in the course of time always more from the adult ancestors, it is *à priori* not clear why this should not be the case also in the embryonic stages." And he argues that the proper method in embryology is to determine first, not what is palinogenetic but what is cenogenetic, because the latter may be more readily ascertained. Indirect develop-

ment is brought about by the necessity to the embryo of securing food; and there may be struggle for existence between larval stages of the same species, resulting in the survival of the fittest. "It appears accordingly probable on the whole that the more perfect in the general sense of the word the metamorphosis is, so much stronger the ceno-genetic modification of the larval forms, and so much more imperfect altogether the genealogical evidence retained in the whole embryology."

Hurst (1893, as quoted by Cope, 1896) argues that in no case is there any close parallelism between ontogeny and phylogeny, but only between the ontogenies of forms derived from the same ancestor.

Wilson (1895) has concluded: "And thus we are brought to a point of view directly opposed to that which on the whole is, I believe, the prevalent one, to the view, namely, that we must primarily take anatomy as the key to embryology, and not the reverse. Comparative anatomy, not comparative embryology, is the primary standard of the study of homologies, and hence of genealogical descent." One strong point in his argument is: "It is a familiar fact that parts which closely agree in the adult, and are undoubtedly homologues, often differ widely in larval or embryonic origin either in mode of formation or in position, or in both." And he maintains "that the persistence of ancestral reminiscences in development or of similarities in the development of homologous parts is in some way connected with the persistence of ancestral conditions of development."

Oscar Hertwig (1898) approaches the subject from his standpoint of the "species-cell." He argues that since the complicated mature stages are determined by the character of the species-cells, and since these stages have had a long descent with modification, it follows that the species-cells

also must have traversed a corresponding development from simpler to more complicated conditions of their finer organization. "Ontogenetic studies give us therefore only greatly changed copies of phylogenetic stages . . . do not, however, correspond to them in their proper content. That certain form conditions recur in the embryology of animals with so great constancy and in a manner agreeing in principle, depends mainly on this, that they under all relations furnish the necessary antecedent conditions, in which alone the following higher degree of the ontogeny can develop itself." This is an attempt to reconcile the recapitulation hypothesis with the idea of epigenesis. In his earlier work on the "Cölomtheorie" (1881) Hertwig was deeply influenced by the *Gastraea*-theory of Haeckel, so that his present stand is a wholesale retraction of his former one.

Morgan (1903) writes: "It is only the embryonic stages of the two groups that we are justified in comparing; and their resemblances are explained on the assumption that there has been an ancestral adult form having these embryonic stages in its development and these stages have been handed down to the divergent lines of its descendants." This view is practically the same as that expressed in the fourth law of von Baer.

We may conclude with the opinions of two great anatomists, Cope and Gegenbaur, because their experienced judgments have done much to influence men's thoughts. The third great anatomist of the past half century, Huxley, will be quoted later. Cope was at once a systematist, paleontologist, and anatomist; Gegenbaur first embryologist, then anatomist.

Cope (1896) writes: "It is evident that 'exact parallelism' can only exist between ancestor and descendant in the same restricted line. . . . So soon as new subordinate characters are assumed, or a change in the order of

appearance of character supervenes, the parallelism becomes 'inexact,' and such is the kind of parallelism usually observed. And it is more inexact the more widely removed in relationship are the forms compared . . . characters acquired during the phylogenetic history are continually assumed by the progressive forms at earlier and earlier periods of life. . . . All progressive organic evolution is by acceleration, as here described. Retrogressive evolution may be accomplished by a retardation in the rate of growth of the taxonomic characters, so that instead of adding, and accumulating them, those already possessed are gradually dropped; the adults repeating in a reversed order the progressive series, and approaching more and more the primitive embryonic stages. This process I have termed 'retardation.' Retardation is not, however, always exact. . . ."

Gegenbaur (1870) at first held: "The becoming explains what has taken place, and embryology, in that it is based on the process of differentiation, shows the compound in its simple beginnings, whereby it allows understanding of relations which in the completed condition are hidden." But as he became drawn more towards comparative anatomy, and noted the theoretical discrepancies between anatomists and embryologists, particularly with regard to his archipterygium-theory of the origin of limbs, he came to discountenance the value of embryology. So he states, in a quotation given by Wilson (1895): "Ontogeny, accordingly, becomes a field in which an active imagination may have full scope for its dangerous play, but in which positive results are by no means everywhere to be attained. To attain such results the palingenetic and the ontogenetic [cenogenetic] phenomena must be sifted apart—an operation that requires more than one critical *granum salis*. On what ground shall this critique be based? Assuredly not by

way of a *circulus vitiosus* on the ontogeny again; for if cenogenetic characters are present in one case, who will guarantee a second case, used for a comparison with the first, does not likewise appear in a cenogenetic disguise? . . . The necessary critique must be drawn from another source," that is, comparative anatomy.

By far the most consistent recent supporter of the recapitulation hypothesis was Kleinenberg (1886), who maintained that "the principles of classification must remain the same whether it concerns the end stages or the intermediate stages of an evolutionary cycle, and when I find in the embryology of an Annelid a form which possesses absolutely nothing of Annelid organization, on the contrary in its essential parts is similar to a Medusa, I take it then not for an Annelid but for a Medusa." This is the very opposite extreme to Gegenbaur!

This historical account has taken somewhat more space than I had intended, but now it is at end and we may examine the recapitulation hypothesis critically.

B. CRITICAL

In the first place, with regard to the supposed process of "pushing back" of adult characters into earlier embryonic stages, which had been called by Lankester (1877) "precocious segregation," and by Hyatt and Cope "acceleration." This really applies only to a character that had been added at the end of an ontogenetic cycle, and the expression is highly figurative and metaphorical rather than exact. Conklin (1905) has pointed out that this idea of a pushing back is erroneous, and that it is rather a case of certain embryonic characters appearing in development earlier than others, and not a case of their being pushed further back from a terminal stage.

Most writers, following Fritz Müller and Haeckel, have

distinguished between palingeny and cenogeny in the history of the individual, or what Cope named, respectively, exact and inexact parallelism. Thus Haeckel reasons that certain stages or characters of the embryo may be recapitulative of ancestors, while others are not. So has arisen the method of Haeckel: to read the phylogeny from the ontogeny, decide first what is palingenetic, and abide by that; or, as Lang put it, take the easier course of deciding first what is cenogenetic. This idea implies that racial change may have modified certain ontogenetic stages, but others to much less extent or not at all.

A little judicious reflection shows this to be a fallacy, and that Hatschek was right when he said "that with the phylogenetic modification of any animal form (individual cycle), never only the end stage becomes changed, but always the whole row from the egg cell to the end stage." He unfortunately failed to follow his own principle. For assuredly no modification of any stage, or particular structure or function, in the ontogeny can become inherited unless its effect be transmitted through the germ plasm of the reproductive cells. And therefore, just as Oscar Hertwig has argued, the egg cell, correspondingly also all the cells developing from it, must become modified. The race is a succession of individuals between the first and last of which differences have arisen, that is, the original inheritance has become modified by variation. Suppose in this series that a modification first appeared in an individual K; then for a succeeding individual L, to show the same or some induced variation, the germ cells of L must first become modified as an indirect result of this modification.

It would make no difference in this reasoning whether the initial variation arose in the soma and came to modify the reproductive cells, or whether it originated in some change of the energies of the germ plasm itself. In any

case a germ cell could not transmit a modification unless its own substances and activities had become changed. For a new racial character is not something, like dead ballast, passively transported by the germ plasm; it is a change in the living processes. The mature egg cell is the commencement of any individual cycle, therefore its processes must become changed if it is to transmit a change. Any other mode of transmission is inconceivable.

Therefore every change in the race means also a racial modification of the germ plasm. But we have seen in another chapter that the species is as much fixed in the egg as in the adult, and that a particular kind or species of germ plasm gives rise always to a definite kind of adult. By the energies of this germ plasm the organization of the adult is brought about. Now since the very first stage of the individual, the egg, has become changed, all subsequent stages must become modified, and not one of them could remain unchanged as in the ancestor where the variation had not yet appeared.

From this it follows that it is impossible for new stages to be added at the end of an ontogenetic series or to become interpolated between other stages of such a series, without causing a modification, in the following generation, of the stages preceding them. A phylogenetic accretion necessitates modification of every stage in the embryology of the descendant, and not only of that stage at which it first appeared. And the egg cell itself must become modified to a degree relatively correspondent with any and every succeeding stage in the embryology, even though the change of the germ cell be far less perceptible than that of a later stage.

Accordingly, where there has been in a race any descent with modification, it is erroneous to attempt to decide in the ontogeny of any of its individuals, between what is a re-

capitulation of the ancestry and what is not. For every stage from the egg to the adult is equally palingenetic or equally cenogenetic. As Cope put it, exact parallelism is possible only between the most closely related forms. Yet he too seemed to make the mistake of maintaining that certain ontogenetic stages may be more palingenetic than others.

The egg of a Mammal is as dissimilar from that of a Fish as their adult stages, no matter whether the differences are as perceptible or not. This was the idea of the great old-master von Baer: the egg is as much a Bird as is the Hen. As it proceeds the individual development leads to the perceptibly more complex; but to produce the complex adult stage of the Mammal the germ plasm of the Mammal must have to the same degree greater complexity of growth energies. The earlier the ontogenetic stage the more the individual may seem to be like its simpler ancestors; but in reality it is just as unlike them in those earlier stages as in its matured condition. For degree of difference must not be adjudged in this case from visible differences alone, but rather equally well from differences in growth energies and ultra-observational structural bases, which, though not perceptible, are nevertheless just as clearly proven to exist.

The organism from the egg to maturity is one and the same species, whether it be composed of one or of several individuals. For it is impossible that one species of germ plasm should engender different species of organisms.

Certain structural characters or stages of an ontogenetic cycle may seem more ancestral than others. Thus the larval stage of an Insect appears more similar to the form generally supposed, from other reasons, to be the ancestor, than does the pupal. Yet it cannot be really more like the ancestor than is the pupa, for its developmental energies must be just as different. The occurrence of such a

clearly cenogenetic stage as the pupa, one which could never have had its counterpart in an adult ancestor, modifies not only that part of the ontogeny which follows it, but, in that it is inherited, implicates a change of the germ plasm, and therefore of the whole ontogeny. Then it must also be kept in mind that modifications of the embryogeny may often be of such nature as to simulate ancestral conditions, be secondary parallelisms; and that is just what an Insect larva is.

It is such deceptive simulation, secondary parallelism or convergence, that has been so frequently mistaken for a palingenetic inheritance of ancestral characteristics.

In a later chapter it will be shown that the method is wrong in principle, to compare an adult stage of one organism with an immature stage of another; incorrect, because it heightens to the maximum the inexactness of the comparison. Yet that is exactly the mode of comparison made by the recapitulation hypothesis.

Two closely related species of Nemertine, as in the genus *Lineus*, may show quite different modes of development, the one continuous and the other discontinuous (larval). More than this, individuals of the same species from different localities may show different kinds of larval development, as in the case of certain Crustacea. We are in no way justified in concluding, from the examination of the embryology alone, that one of these modes is more ancestral than the other. And the one which might appear for other reasons to be more palingenetic may really not be so, but a secondary convergence. Gegenbaur was quite right in his general contention that no racial descent can with any degree of certainty be decided from the analysis of ontogeny, when ontogeny is used as a basis of comparison, for that amounts to reasoning in a very small circle.

Therefore we can only conclude that the embryogeny does

not furnish any recapitulation of the phylogeny, not even a recapitulation marred at occasional points by secondary change. Where there has been descent with modification, the ontogeny exhibits cenogenetic change at all stages and no exact palingeny at any one stage. The supposed palingeny is partly imagined, partly assumed to exist from *a priori* considerations. Where there is similarity it is probably quite as frequently similarity from convergence, or secondary simulation, as from any inherited likeness. An analysis of the stages during the life of one individual can in no way present a knowledge of its ancestry; and the method of comparing non-correspondent stages of two species is entirely wrong in principle.

C. LARVAL HOMOLOGIES

In this connection we may discuss the value of larval theories, and in particular one of them that has become quite famous in its influence upon embryological speculations, the Trochophore-theory. To properly understand its content it is necessary to trace its origin.

The researches of Wolff (1759), Pander (1818), and von Baer (1828) demonstrated that the parts of the Vertebrate individual develop from two primary germ layers. Von Baer distinguished four plans of development of these layers: the peripheric (Radiata), the massive (Mollusca), the longitudinal (Articulata), and the doubly-symmetrical (Vertebrata). Kölliker (1844) compared the modes of development as follows: (1) the embryo arising from a primitive part, then either (a) growing in two directions with bilateral symmetry (Vertebrates, Articulata), or (b) growing uniformly in every direction (Molluscs); (2) the embryo arising simultaneously, then (a) in the direction of its transverse axis (Echinoderms, Acalephs, Polyps), or (b) in the direction of its longitudinal axis (Worms).

Vogt (1851) based a classification upon the position and amount of the yolk of the egg. Then P. J. van Beneden distinguished Hypovitellia, where the yolk (vitellus) enters the body from the ventral side (Vertebrates); Epivitellia, where it enters from the dorsal side (Articulates); and Allovitellia, where it enters neither from the dorsal nor from the ventral side (Mollusco-Radiaria).

These were the principal of the early embryological classifications, and were the first expressions of the idea that classification should consider mode of development.

A new thought came in when Huxley (1859) compared the two body layers of an adult Medusa with the two primary germ layers of the embryo of a higher form. Allman (1853) had named these layers in the Medusa ectoderm and entoderm, and these names, or the equivalent ones, ectoblast and entoblast, have since been applied to the germ layers also. Huxley's interpretation proved so significant that I cannot resist quoting from the original. "The peculiarity in the structure of the body-walls of the Hydrozoa . . . possesses a singular interest in its bearing upon the truth (for, with due limitation, it is a great truth), that there is a certain similarity between the adult states of the lower animals and the embryonic conditions of those of higher organization. For it is well known that, in a very early state, the germ, even of the highest animals, is a more or less complete sac, whose thin wall is divisible into two membranes, an inner and an outer; the latter, turned towards the external world; the former, in relation with the nutritive liquid—the yolk. The inner layer, as Remak has more particularly shown, undergoes but little histological change, and, throughout life, remains more particularly devoted to the function of alimentation, while the outer gives rise, by manifold differentiations of its tissue, to those complex structures which we know as in-

tegument, bones, muscles, nerves, and sensory apparatus, and which especially subserve the functions of relation. At the same time the various organs are produced by a process of budding from one or other, or both, of these primary layers of the germ. Just so in the Hydrozoon; the ectoderm gives rise to the hard tegumentary tissues, to the more important masses of muscular fiber, and to those organs which we have every reason to believe are sensory, while the endoderm undergoes but very little modification. . . . Thus there is a very real and genuine analogy between the adult Hydrozoon and the embryonic vertebrate animal; but I need hardly say it by no means justifies the assumption that the Hydrozoa are in any sense arrested developments of higher organisms. All that can justly be affirmed is, that the Hydrozoon travels for a certain distance along the same great highway of development as the higher animal, before it turns off to follow the road which leads to its special destination."

Then Kowalevsky (1871), one of the greatest comparative embryologists of all time, published his observations upon the embryology of Insects, Annelids and *Sagitta*, and concluded that the two primary germ layers of Vertebrates are homologous with those of other groups. "I hold the view to be not maintainable, that the organs of animals of different types cannot be homologous."

Such was the growth of the germ-layer theory, which may be expressed: the organs of all animal groups develop from two primary germ layers, and in all groups ectoblast is homologous with ectoblast, and entoblast with entoblast.

The next step was taken by Lankester (1873) and Haeckel (1874), who sought to place the theory upon a yet firmer and more extensive foundation. Lankester introduced the Planula-theory: that as a common embryonic stage in all animals is to be regarded one essentially similar to the

two-walled, ciliated, free-swimming and mouthless larva of many Hydrozoa, and that this repeats an ancestral racial condition. While Haeckel imagined the double-walled and invaginate gastrula stage as common to all groups, and repetitive of a hypothetical ancestor, the *Gastraea*, a simple double-walled sac less complex than the modern *Hydra*. Haeckel has developed this *Gastraea*-theory more fully in later publications, and it has found more followers than the Planula-theory; yet there are many who consider, and with good reason, the Planula to be a more primitive embryonic condition than the invaginate Gastrula.

These two theories were stimulative to the hunt for homologies between still later stages. And a host of enthusiastic observers, most prominent among them Kowalevsky, Metschnikoff, Claparède, Kölliker, the two van Benedens and Balfour, began to make known the outlines of the early embryology of many animal groups, for the most part the early stages of marine animals up to the appearance of the larva. So in addition to searching for homologies between germ layers, and between gastrula and planula stages, men began to compare the later larval stages, and on the basis of the recapitulation theory to found upon them interpretations of genetic descent. The number of such theories is great, but we will discuss only the central prominent one, the Trochophore-theory.

The chief founder of this theory is Hatschek (1877, 1880, 1888). The free larvae of various marine Annelids show remarkable uniformity of structure, and the larvae of Molluscs and Bryozoa resemble them quite closely in such characteristics. All these larvae are considered to be slight modifications of one kind of larva, called by Hatschek the Trochophore. The theory is that all such larvae are repetitions in the embryology of an hypothetical ancestral form, the *Trochozoön*, which in its adult condition is supposed to have been

closely similar to the Trochophore larva of its racial descendants. All animals, accordingly, which possess such a type of larva are supposed to have transmuted from such a common ancestor.

An excellent formulation of this theory is given by Hatchesek in his "Lehrbuch," and good critical treatments of it, from different points of view, by Eisig (1887) and Lang (1903); consequently it would be superfluous to enter here into a discussion of all of its details. The greater number of embryologists may be said to favor the theory in one form or other.

The argument for the theory is twofold. First, that larval development is more primitive than direct development; and, second, that the close structural agreement of larvae of different animals can be interpreted singly to imply community of descent of the forms possessing such larvae.

That any one stage of the ontogeny parallels the phylogeny more fully than any other stage is, as we have tried to prove, scientifically untenable, because any inherited modification must come to affect all stages of the individual. There is also no good reason to consider that racial modifications become added only at the terminal stages of the ontogeny. For modifications may arise at any stage of the individual, and indeed the earlier they appear the more apt they would be to become inherited, because they would be more likely to profoundly affect the organization. For these reasons the recapitulation hypothesis gives no foundation at all to the Trochophore-theory.

The second line of argument is perfectly justifiable, since it compares corresponding stages of different animals, and from their similarity of structure reasons similarity of descent. This is the method of comparative anatomy. But it is first necessary to inquire whether these structural agreements may not be better interpreted as due rather to agree-

ment in mode of life than to community of racial origin. That is to say, may not such similarities be convergence phenomena, or simulations? For where there is community of structural relations without pronounced agreement of habits we can be reasonably sure of ancestral community; but we cannot be so positive when both kinds of agreement concur.

There can be little question of the essential anatomical resemblance of the various Trochophore larvae; that has been sufficiently demonstrated by Hatschek and his followers, if somewhat overrated; consequently we need not go over all that evidence. Such larvae belong almost altogether to marine species, and the lamellibranch Mollusc *Dreissensia* is the only known freshwater form that has a Trochophore in its development; this exceptional species has only recently taken up limnobiotic existence. Then sometimes in different species of the same genus of marine Annelids a Trochophore stage may occur or may not. This shows that the larval stage, if ancestrally present, can become readily lost. If the free-swimming larva were the repetition of an ancestral adult condition, why should it not be equally conserved in marine and freshwater life? Surely the only answer can be that the difference is due to environmental conditions. Supporters of the Trochophore-theory argue that freshwater life has caused the loss of the larva; accordingly they admit that environmental influences modify the development and mar its value as a record of the ancestry. But if change of the environment can engender loss of stages it could equally well produce new modifications, so that from this point of view alone freshwater development without a larva might be as primitive as marine development with one. That is, the Trochophore might be a secondary condition.

Then it is known that among marine forms larval stages are there most pronounced, where the adult is sedentary, or

has a comparatively slow mode of locomotion. So in most Molluscs, tubicolous Annelids, sessile Bryozoa, *Phoronis*, Echinoderms, etc. But in typical pelagic animals there is usually no sharply demarcated larval stage, because the mode of life of all the stages remains approximately the same.

It was pointed out in the first chapter that pelagic existence is probably not as primitive as littoral, but that life upon or near the sea bottom, within the region of light, is more primitive. Now, all the groups in which a Trochophore larva occurs are essentially littoral in their habits. Therefore it follows, as the simplest and nearest interpretation, that this larva is an adaptation, a modification suited particularly to insure the dispersal of the species and to prevent the overstocking of the homestead. Why should not more of the animal groups possessing a Trochophore be pelagic, if they had been derived from a pelagic ancestor? Perhaps the lack of a Trochophore in freshwater species is due to the danger of such a motile stage in the freshwater since such a larva would run the risk of being carried by currents to the sea, and so becoming exposed to death from contact with the salt water; but this suggestion is speculative. We do not understand why freshwater forms of Annelids and Molluscs have no larvæ; but we can readily and reasonably explain why slow-moving bottom animals of the sea should possess them: they would be adaptive stages of great value in maintaining the species.

From such considerations, and especially when we disregard the recapitulation theory, as we are bound to do, the Trochophore larva cannot be satisfactorily explained as a repetition of an ancestral stage.

Then the theory might be so modified, as some embryologists have done, to read: the presence of a Trochophore larva in so many diverse groups proves that the ancestors of all these groups, while not necessarily like a Trochophore larva,

must nevertheless have possessed such a larva. Yet for this idea the basic foundation is again the recapitulation hypothesis! And if it were true it would be of no service in determining racial descent, because it throws no light upon the adult condition of the ancestor.

The similarity in the structure of the larvae of Annelids, Molluscs and Bryozoa is indeed striking. All have a bilateral form, an angularly bent intestine, an apical sense plate, one or two ring nerves in connection with circular muscles; and the latter are beneath circular thickenings of the ectoblast that bear cilia, these rows of cilia, trochi, giving the larva its name of "hoop-bearer." Frequently there is a pair of simple nephridia, the anus is dorsal, there may or may not be present a pair of coelomic sacs, and there is frequently a tuft of long sense hairs at the posterior end. Then there is a large cleavage cavity (archicoel) with larval-mesoblastic muscles and nerves. Such a combination of characters in the larvae of different groups could not be readily interpreted, except on the basis of similarity of descent. Yet the presence of an apical sense plate at the end that goes foremost in the path of locomotion is mechanically as understandable as the fact that all elongated animals moving in a straight line, with one end (the head) always in front, should have a brain at that end. For as it is the end that soonest comes into contact with environmental objects, it is the one most stimulated to sensory reaction. The adults of all these groups have nephridia and an intestine, so it is not surprising that their larvae should have had them too. And as for the agreement in the arrangement of the ciliary rings upon the surface of the body, that is almost exactly paralleled in some members of groups that certainly never had any connection with a *Trochozoon*, namely, the Infusoria. In a number of motile species of these Protozoa there is a ring around or in front of the mouth (cytostome), and one or several rings

behind it. Thus the external configuration and ciliary arrangement of some Protozoa is remarkably similar to that of Trochophore larvae. In Trochophores of closely related Annelids there are marked differences in ciliation, so that only the ring of cilia in front of the mouth, the prototroch, remains relatively constant; the perianal ring is very variable, and also the ventral ciliated tract.

The Trochophore-theory has generally included also the view that the Rotatoria approach closest of all to the hypothetical *Trochozoon*, and that they may be regarded as Trochophore larvae become sexually mature. The most detailed statement of this idea, and argument for it, has been presented by Zelinka (1891). But I would agree with Lang (1903) that there has been too much said about larvae becoming sexually mature; for if the body tissues should become arrested in their growth, why should the germ cells go on developing? While there are a number of marked likenesses between Trochophore larvae and adult Rotatoria, there are at the same time a number of constant differences, and these are too frequently overlooked. Thus no Rotatorian is known to possess ring nerves, nor a ciliated groove between the mouth and the anus. The reproductive organs of Rotatoria are quite different from those of any of the groups in which Trochophore larvae occur; and, further, they are neither simple nor embryonic in character. Then Rotatoria show as characters not possessed by Trochophore larvae: the lateral sense organs, the opening of the nephridia into the cloaca, the locomotory foot, the separation of the cerebral ganglia from the skin (hence really no apical sense plate), the apical rather than ventral position of the mouth (this not always the case), the presence of a complicated chewing apparatus (mastax), and the anterior displacement of the anus when a foot is developed. The structural resemblances are accordingly not nearly as close as generally sup-

posed. And there is another consideration of quite equal weight, and it should not be neglected. The Rotatoria are essentially freshwater forms, while Trochophore larvae are stages of marine animals.

That particular Rotatorian, *Trochosphaera aequatorialis*, which shows the greatest external resemblance to an Annelid Trochophore, is probably a highly specialized form and by no means primitive or ancestral; yet it is particularly with this species that Trochophores have been compared.

For these reasons the group of the Rotatoria does not add any strength to the Trochophore-theory, nor is there good reason to include its relations in the theory. And there is a further argument why they should not be regarded as related to the animals having Trochophore larvae. The development of the Rotatoria is direct; they have no larvae. But if they were related to *e. g.* Annelids, we should expect a stage somewhat similar to the Trochophore larva to occur in the development of a Rotatorian.

The recapitulation hypothesis is scientifically untenable, and where there has been transmutation of species, the embryogeny, neither in whole nor in part, exactly parallels the racial history. The relation between the two is always that of an inexact parallelism. Considerations based upon any such idea of recapitulation are erroneous, and therefore of no help in determining racial descent.

CHAPTER VIII

MORPHOLOGICAL COMPARISONS

WHAT the method of comparison should be is, of course, the cardinal puzzle in any science. The philosophical logician points out that conclusions may be reached by enumerative induction, or by analogy; and he goes on to distinguish different kinds or grades of analogies. But the idea of a "true" analogy cannot be sharply defined, and indeed it is probable that the form of an analogy, or comparison, must differ with the subject matter. As Gegenbaur (1898) has put it: "Out of the theme the method determines itself." When carried to its limits, all reasoning will be found to be a *circulus vitiosus*, since all our perceptions, hence the ideas founded upon them are limited in number and defined by their interrelations. The logician has failed to present formulations that will help the biologist in his comparisons, for the very reason that he, too, can think only in comparisons, and cannot sharply define or justify his definitions. And it is hardly necessary to state that all those attempts have been failures, which have tried to express complex vital phenomena in any concise mathematical form.

And yet no fact is more obvious than this one, that phylogeny must look to its methods of comparison if it is to have confidence in its results. Our theoretical conflicts are due very little to differences in observation, to the subject matter of discussion, mostly to the evaluation of the phenomena. Progress in phylogeny will come quite as much from improvement in the method of comparison as from enlargement of the phenomenal foundation. Universal con-

sensus of view is not expected, for "as many doctors, so many opinions." But the lack of a generally consistent method is keenly felt by all phylogenists, and the present babel of opinions is producing a stagnation in the circulation of the results.

A. HOMOLOGIES

Organisms should be considered in their entirety and at all periods of their ontogenies. By comparison their likenesses and differences become apparent, and our subject matter is just these relations. The general working principle is that likenesses indicate community of descent. The more similar two organisms are, the greater is the probability of their genetic relationships, on the idea that if two be entirely similar they must undoubtedly be very closely related. Correct as this principle is in general, its application must be made very circumspectly: there must be great care in the judgment of what are likenesses. For the closest possible relation is between offspring from the same parents; yet a female of one species frequently appears to differ far more from a male of that species than from a female of another, at least in so far as the differences are perceptible.

This shows, it may be parenthetically remarked, that to be correct in instituting comparisons it is necessary to consider all kinds of individuals composing what may be termed an offspring unit, that is, the offspring group of one parent, in comparing one species with another. It would be incorrect, because disregarding whole individuals, to seek to establish genetic descent on *e. g.* males alone, or females alone, or upon sexual rather than asexual individuals.

For essential likeness in structure. Owen (1846) introduced the morphological idea of "homology," and distinguished as a "homologue, the same organ in different animals under every variety of form and function." And in

another place he stated (1848): "Homological relationships . . . are mainly, if not wholly, determined by the relative position and connection of the parts, and may exist independently of form, proportion, substance, function and similarity of development." Owen, like his cotemporary, Louis Agassiz, was actuated in his thought by the idea of the "type of structure" as founded by von Baer and Cuvier; and to him homology meant simply an indication of type community, not of racial descent. The word homology is now in use to denote a relation of genetic affinity, and we will adopt the signification given it by Hatschek (1888): "We call homology an agreement that rests upon common descent of the organisms concerned. The expression homology is used accordingly quite in the sense of homophyly." And so we will employ homology, with the basic idea of community of descent, in the place of Owen's concept of unity of type.

In attempting to read homologies, indications of genetic affinity, everything depends upon the method of comparison. For one will see a likeness where another finds a difference, and both may disagree as to the amount of each kind of resemblance.

B. COMPARISON OF WHOLE ONTOGENIES

The unit of study in phylogeny should be the whole organism, not a part of it, nor yet a group of organisms. It is further not an arbitrarily selected stage, as the larva or the adult, that is to be considered and weighed, but the whole life cycle.

More is perhaps to be learned from comparisons of mature, more perceptibly complex stages than by those of earlier embryonic conditions; we shall return to this question. But the species is as much fixed in the egg as in the adult, though in the former its characters are generally not so perceptible. And for this reason, as for the more impor-

tant one that understanding of definitive form is greatly aided by the knowledge of its embryonic formation, it is clear that the whole life cycle must be considered. Phylogenetic interpretations based on purely embryological evidence are on this account imperfect, just as those founded entirely upon criteria of adult structure; both omit a great mass of phenomena that should be weighed and measured.

The facts of morphology are phenomena of structure; this structure is but a result in a series of growth changes, and there is neither reason to treat of structure only at its terminal stage, when it has ceased to change, nor only at an earlier time, before the process has been completed; for to do either would be to place entirely arbitrary limits. The understanding of an organism implies a knowledge of all its stages, to the morphologist, then, of all those structural differences that are perceptible accompaniments of these stages. No adequate comprehension of the racial genesis can be achieved unless full attention be given to the whole life cycle.

There can well be no valid objection to this general principle, which has been stated before: phylogeny is a comparative study of ontogenies, of whole ontogenies and not selected portions of them.

We are as yet indescribably far from an understanding of any one complete life cycle. The nearest approach to it has been made in the case of certain Protozoa, but ontogenies of the Metazoa are but incompletely known, even the most thoroughly examined cases of *Hydra*, *Ascaris*, the Frog and the Chicken. The body of morphological evidence now open to the judgment of the phylogenist consists to greater part of phenomena of adult structure, to lesser part of facts of embryology, and the latter embrace to great extent only the earliest stages.

The comparative anatomist and the embryologist have

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in some cases come to regard themselves as competitors, if not opponents, since each is apt to underestimate the value of the other's results. This is a fault of misunderstanding. This conflict of view has been, however, most beneficial in demonstrating that there must be errors in the method of study, for it is evident that in a quarrel one, if not both, must be wrong. Really both are wrong just in so far as they neglect to consider the whole series of the ontogeny. From the very incompleteness of the data from which we reason, all our conclusions must be considered merely tentative, awaiting final proof.

Now, an ontogenetic cycle may be completed within the lifetime of one individual, as in continuous development and in discontinuous development of the ekdytic kind. But it may also in other cases extend over the life periods of more than one individual, as in metagenesis and heterogenesis. The former is a simple and the latter a complex cycle. In the case of the latter it is clear that phylogeny has to treat not only the ontogeny of any one particular individual of the cycle, but also the ontogenies of all the series of individuals. For both simple and complex cycles are progresses from a beginning to a definite end, and the whole succession must be considered in both cases if we would understand them thoroughly. There are certainly great difficulties in the application of this principle, as in making a comparison between the life history of a monogenetic and a digenetic Trematode: one presents a greater series of individuals than the other, even successive processes of cleavage. Yet just such a comparison serves to elucidate what is in the ontogeny common to the two and what is restricted to the one, and so presents the most thorough basis for gauging the adult forms. Were we to select the ontogeny of only one individual of a metagenetic cycle for comparison with the ontogeny of the only individual embraced in a simple cycle we

would be neglecting in the former a great series of phenomena; in other words, we would omit evidence that should be adjudged.

In the next chapter attention will be given to the question of the relative value of morphological characters in the determination of descent. Here the decision must be emphasized that not only should the whole life cycle be studied rather than an arbitrarily chosen part of it, but also all structural characters. A consensus of opinion is being reached in this matter, but very slowly. There have been some very brilliant and stimulating attempts at racial analysis, based upon a certain set of characters. Such was Huxley's (1867) classification of Birds, which considered mainly the peculiarities of the palatal region of the skull; von Jhering's (1877) arrangement of the Molluscs according to the relations of the nervous system; and Linnaeus' (1858) systematization of the Insects according to the structure of their wings. But the method in such work is wrong, whatever the results may be, in that it brings into examination only a portion of the organization. Lereboullet, in a classical monograph (1848) put this clearly, in stressing the necessity "of not forgetting that the natural method of classifying organisms is by the totality of their relations and not by such or such isolated characters." This method is fully and for the same reason as unjustified as classification based upon types of larvae (as Trochophore homologies), or upon modes of development of particularly selected parts (coelom-theory of the Hertwigs). All characters should be considered and in all stages of their formation; then comparisons with other organisms can bring out their relative values. Before this comparison has been made a morphologist has no logical right to base phylogenetic conclusions upon only few characters: he has not the right because he has not determined their value.

C. COMPARISON OF CORRESPONDENT STAGES

There is one method in comparison that will make for greater uniformity of conclusion, if it be consistently followed, and if it can be rationally justified. It is the method of comparing organisms or their parts at corresponding stages. Any and each Metazoan ontogeny shows two stages that may always be distinguished, the egg cell and the terminal mature stage. It is always a correct comparison, the one between mature stages of two organisms, or between their initial stages; for it is a comparison of states which bear the same relative value, hold the same relative position, within their respective ontogenies.

An exact comparison, to be sure, can be made only between two organisms that are precisely similar, and phylogeny in dealing only with the relations of organisms that are more or less different can, on this account, not expect to reap any exact comparisons. But the degree of the inexactness can be minimized by comparing only correspondent stages. If we regard a single ontogeny composed of stages *a, b, c, d, e*, we conclude that *e* is more closely correspondent to *d* than to any of the other stages, for the reason that it is separated from it by a smaller degree of change. In one and the same individual those stages can be most exactly compared which are nearest each other with regard to their position in the life cycle. And in weighing different individuals we must also compare stages that are relatively correspondent within their respective ontogenies, for only such stages have a commensurable value that is to some extent exact.

One frequently hears the expression that the mind of a Dog cannot be compared with that of a Man, but only with the mind of a Child. Such comparison of adult stages of lower organisms with embryonic states of higher ones is of

course the method in the recapitulation theory, and is responsible for it. The radical error of this hypothesis was pointed out upon a preceding page, where it was shown that a higher animal does not in the course of its embryogénie repeat its ancestry, because any inherited racial change must modify every stage of the embryology. The same error is at the bottom of many morphological explanations, of many nursery tales of the anatomist to which we were brought up. To compare stages of two organisms not bearing the same relative position within their respective cycles, *i. e.*, stages that are not correspondent, as we use the word, is then to compare conditions of different degrees of perceptible differentiation. Adult may be compared with adult, because they are equivalent as terminal conditions, and similarly egg may be compared with egg, because each is a beginning. But to compare an egg, or any early embryonic period, of one individual with the adult of another, is to heighten to its maximum the inexactness of the comparison.

Processes of embryogeny differ both in kind and in degree, and some ontogenies are longer or more complex than others. But all show an agreement in the progress from that stage (egg) having the greatest power of reproduction, to the one (adult) in which the body cells no longer reproduce. These extreme stages offer the most exact comparisons between different animals. In all cases it is facile to compare egg with egg, because these stages are readily determinable. It is somewhat more difficult to compare adult with adult, on account of the difficulty in deciding exactly what is the adult in every case. For this stage may coincide with sexual maturity, as notably in those forms (*e. g.*, many male Insects) which have as a rule only one such period, and die immediately after copulation. Frequently the individual shows successive reproductive periods, temporally separated, and its body may undergo continued

change up to the last period; that is what occurs in most Vertebrates; in such a case sexual maturity could not be taken as the criterion of the adult state. We might specify the adult state as that one, which may accompany or may follow sexual maturity, at which the somatic development has reached its conclusion and before senile changes have set in. The adult then would be the end of the somatic ontogeny, and if it be so defined, there need be no further discussion of what constitutes maturity. And indeed this is the only justifiable definition of adult, the stage of the end of somatic growth.

There now comes up the matter of comparing in different organisms stages that are neither the initial nor the terminal ones. The correct principle is to compare only correspondent stages, defining as correspondence relative equivalence with regard to embryological sequence of process and structure. The first and last stages are fixed and secure points for comparison; the correspondence of intermediate stages must be determined for each case. So the larva of one need not be correspondent to the larva of another form, in the event that they come at different relative periods of their respective ontogenies; just so the time when one foetus breaks from its membranes need not be correspondent to the birth of the foetus of another species. The more genetically remote two organisms are the less must necessarily become the exactness of their agreement, and the greater, accordingly, the difficulty of ascertaining what intermediate stages of the two are relatively most correspondent. Sometimes, even in what are evidently closely allied forms, one species may exhibit an ontogenetic condition, *e. g.*, a specialized larva, wholly absent in the other. In such an example the larva of one cannot logically be compared with any step of the other's growth cycle. Such cases are numerous enough, and we need simply adduce the Annelid genus

Nereis and the Nemertine genus *Lineus*. Further, the more removed a stage is from the initial one of the egg, or from the final one of the adult, the greater becomes the difficulty of finding what intermediate stage of a different organism is its nearest correspondent.

But whatever organisms are being compared, they must be compared at relatively correspondent stages, correspondent in the sense we have just defined the word, and not in its usual physiological meaning. There will be difficulty in determining what stages are correspondent, but this difficulty must be met before a scientific comparison can be made. For unless the comparison is so made, our interpretations must be so inexact as to have little value.

Of interest in this connection are the results of the study of cell-lineage, the investigation of the origin, position, movements and ultimate fate of the cleavage cells of the egg. The important bearing of these painstaking and minutely accurate researches upon problems of differentiation and heredity were touched upon in another place, and do not concern us at present. Such studies have been carried out upon the eggs of various Annelids, Molluscs, Turbellaria, Nemertines, Sipunculids, Rotatoria, Crustacea, Tunicates, and *Dinophilus*. And they have brought to light certain apparently remarkable agreements in the cleavage processes of Molluscs, Annelids and Nemertines, and less complete agreements with those of Turbellaria.

Thus Conklin (1897) sums up the more important resemblances in the cleavage of Molluscs (both Lamellibranchs and Gasteropods) and polychaetous Annelids: (1) In the number and direction of the cleavages up to the 28-cell stage. (2) "In general the cells formed are similar in position and size." (3) "The three quartettes of micromeres are ectomeres" (formed from the ectoblast). (4) "The mesoblast is formed from the cell 4d." (5) The first somato-

blast " has exactly the same origin and position and a similar history," and (6) " it gives rise to a growing-point and a ventral plate." (7) " The rosette series of the gasteropod is exactly like the cross of the annelid in origin, position and probably in destiny." (8) The trochoblasts are equally similar to the turret cells. (9) Formation of a sense organ by the apical cells. (10) Similar origin of the oesophageal ganglia. (11) " The fourth quartette . . . contains mesoblast in quadrant D, but is purely entoblastic in quadrants A, B and C." (12) There is a fifth quartette consisting of entoblast only.

Conklin takes the stand, previously stated somewhat guardedly by Wilson, and sustained also by a number of later students: " I believe there is no escape from the conclusion that the protoblasts of homologous organs are as certainly homologous as are the organs to which they give rise, that the protoblasts of homologous layers are as surely homologous as are those layers, and that the protoblasts of definite regions are as much homologous as those regions." And before him Lillie (1895) reached the conclusion, " that the only safe test of homology in such cases is the end result."

This appears to me the correct way of regarding homologies of cleavage cells. Cleavage cells of different species are then to be called homologous when they give rise to parts that are homologous. From adult relations these cells are to be adjudged, and not adult parts from the relations of the cells.

It would be quite possible that in two diverse forms the steps of the earlier development might be approximately similar in regard to direction and kind of cleavages, size and relative position of the blastomeres, formation of the germ layers, etc., and yet the cells of, *e. g.*, the tenth cleavage in one be not relatively correspondent, as we em-

ploy this term, to cells of the same generation in the other. For let us, for the sake of argument, assume that the adult of one form is composed of 10,000 somatic cells, and that of the other of 100,000. Then, *ceteris paribus*, the 10-cell stage of the first would be ontogenetically really more advanced than the 10-cell stage of the second, be closer to the mature condition; it would be more correspondent to the 9-cell stage of the second. So even apparently exact agreements of blastomeres in the characters mentioned need not imply exact correspondence. Treadwell (1901), more critical than most cell-lineagists, has emphasized various degrees of inexact correspondence of this kind.

Unless the stages compared are relatively correspondent, resemblances between them cannot be regarded as indicative of homology. The 1-cell stage is correspondent in two organisms; the 2-cell stage less so, and the 4-cell still less; these differences increase up to some point in the ontogenies, then begin to gradually approximate towards the adult stages, which are again correspondent.

The term cell-homology has not always been used cautiously. Cell-resemblance should be employed instead until homology is determined, *i. e.*, a resemblance due to community of descent of the animals concerned. Because correspondences occur between cells of the same generation of two organisms, homology is by no means proven, not until these cell generations are demonstrated to be relatively correspondent in the sense in which we defined this word.

And with regard to the famous germ layer theory of Huxley and Kowalevsky, broached in an earlier chapter, we can say that there is indeed a resemblance between the outer germ layers (ectoblast) in all groups, and one also, though less *frappant*, between the inner germ layers

(entoblast). But is this after all a very fundamental agreement? For since the egg cleaves into numerous cells, and these are prevented by the tension of the vitelline, or some other, membrane from arranging themselves in one plane, they are ultimately bounden to form a cell mass of more than one layer. These layers must be either upon the outside or in the inside of the embryo, because every living being must have an outside and an inside, *sit venia verbo*. What is fundamental is the fact that certain definite organs arise from the ectoblast, and different ones from the entoblast; not that one layer is external and the other internal. If the organs which arise from these layers be not homologous, then these layers cannot be, and on the other hand organs may be homologous and yet arise from different cell layers; and here attention is asked to those somewhat numerous cases where in sexual reproduction an organ arises from one cell layer, but during asexual reproduction and regeneration from another.

This discussion might be almost indefinitely extended. But the single point I wish to make is that only corresponding stages should be compared. Unless this method be consistently followed, we shall continue to flounder along in that quagmire of contradictions of which the past has furnished an oversufficiency.

D. THE SYNTHETIC METHOD

Another principle in comparison is to proceed from the more similar to the more unlike. Just as we have found that the relatively most exact comparisons can be made between corresponding stages of ontogenies, so also the relatively closest can be drawn between those organisms that are most alike, most similar because of greatest genetic affinity. The obviously correct method, wherever possible, is the synthetic one of first determining interrelationships

of more intimately connected forms, and so step by step in the process to ascertain broader affinities. Were all animal forms evolved by a process of continuous and gradual development, and did we know all the species of the great range of transmutation, such synthetic establishment of lines of descent would be really a much simpler task than it actually is. But there is good reason to believe that all development has not been continuous. And further, the animal forms accessible to study, even together with the fossil remains of skeletons, are but a fragment of the enormous genealogical arborization, only racial stages at the end of this vast succession. Not sufficient emphasis has been placed upon this point, that the now existent life is a quantity almost incomparable with that which preceded it, and that the million or more known extant species are probably but a drop to the vital ocean from which they have descended. Repeatedly great phyla may have become extinct; and of many of them paleontology finds no trace. This is the weightiest consideration of all against the hope of determining relationships. But racial affinities may nevertheless be worked out with a high degree of scientific probability, though ancestral connectant forms should continue to remain undiscovered, if only the method of comparison be correct.

Yet even though transmutation may have been in some cases discontinuous, and though the forms open to examination represent but a disappearing fraction of the whole totality of life, the synthetic method is nevertheless the right one.

Let us suppose a morphologist is endeavoring to find the affinities of the *Acanthocephala* to the *Nematoda* on the one hand, and to the *Trematoda* on the other; this to be taken simply as an example of the very frequent tripodal anatomical comparison. He might then select a single representa-

tive of each of the three groups for comparison. But the correcter synthetic method would be first to make a comparative study of each of these three groups by itself, a monographical treatment of all the principal forms of each; and then commence the comparison of the larger groups. Such synthesis alone could make known all the members composing a group, thereby fix its boundaries and range of structural variety. The objection is valid that no one man could do all this. Yet it can be done by the combined efforts of many workers. Only such detailed comparisons can indicate those connectant forms so dear to the phylogenetist, and show what is fundamentally characteristic of a group. There must always be great uncertainty about the affinities of remoter forms until closer relationships are first determined.

Any comparison based at random upon a single species, as representative of a larger group, can have little value until it has been shown by a preliminary investigation that it is a particularly generalized form. And indeed the idea of a single species as "typical" of a varied and multiform group is absurd. When the laboratory textbook selects a Lobster as typical of the Crustacea, it gives the student a fallacious and harmful conception of the group; for is not a Daphnid or an *Asellus* equally well a Crustacean? And the student thinks he understands the Molluscs from a study of a Mussel or a Clam alone, though he never comes to see a Snail or a Slug. And when the *soi-disant* guide to the beginner tells him how to dissect the Cockroach, do we not have it on better authority: "look to the Ant, thou Sluggard!" A little reflection shows that some forms of a group are more generalized than others, but they need not on that account be more representative.

The fundamental characters of any natural assemblage of organisms are not known, and cannot be predicated any

more than its boundaries can, until it has first been settled exactly what forms compose the group.

In the matter of certain animals, as notably the Birds, marked by great uniformity of structure, there has been passed the earliest synthetic stage of morphological inquiry. But this does not imply that the synthetic method is no longer serviceable and desirable, or that it has not yet to be applied to other groups. First is to be determined the offspring-unit, the assemblage of the young of one parent, which can be ascertained empirically, and it is the only group that can be so determined; then is to be determined the next higher group, the species. One proceeds thereby from cases of demonstrable genetic community to those where such affinity can be made out by analogy alone. By comparisons of the smaller units, of which the individual is the first, one gradually constructs a knowledge of larger assemblages.

Many an anatomist would remark that this principle is quite generally acknowledged. That is true. But on the other hand most men consciously or unconsciously neglect this method, in hastening to broader generalizations without considering the stepping stones. No man can formulate an adequate knowledge of any group by the study of only a single member of it, no matter how intensely and thoroughly he examines this member; from such a study alone he has no logical right to conclude what is fundamental to the group. Yet many make just this mistake. What is needed is much more exhaustive monographic study of small groups, rather than of single species.

A comparative treatment of a few closely related species teaches much more of transmutation than detailed comparisons of widely separated forms. All of us have been sinners in this matter because of eagerness to rush to broad conclusions. And yet a survey of the morphological litera-

ture shows that monographs of circumscribed groups have been on the whole the most important contributions, just as they are for the most part the more permanent portions of our literature. On work of this nature our final phylogenetic concepts will be based.

The argument in no way implies that broader generalizations should not be attempted before this detailed basis has been laid down. Indeed such broader, if more superficial, treatments are of the greatest importance in suggesting what particular detailed studies could be most profitably pursued. Only let us never forget that they are but preliminary working hypotheses! Even a ten-page discussion of the origin of the Echinoderms, for example, of which there have been a good many, replete with diagrammatic illustrations of imaginary ancestors, weird and uncouth enough to have lived in those primeval seas which we shall never know, may have its uses. Much more important such views as the trochophore-theory, wrong as they are in method, for their stimulation to research has been very great. As examples of the synthetic method that have proved of great value to the phylogenist may be mentioned two very different studies: Leuckart's investigations of complex life cycles and de Vries' analysis of the races of *Oenothera*.

E. ESTIMATION OF THE RELATIVE VALUES OF CHARACTERS

We perceive likenesses and differences between organisms, and these are the bases for our comparisons. The chief part of the search is for resemblances. What constitutes a likeness and what a difference cannot be predicated, but must be brought out in the course of the examination. Thereby many apparent differences may be found to be at bottom likenesses. In the study we generally proceed by comparisons of three or more forms, whereby one is used, in a sense, as a gauge of measurement of the others. For

the investigation of two forms by themselves would not present any scale for comparison. There must be considered at the same time at least a third object; and the more, *ceteris paribus*, the safer would be the reasoning. This is of course perfectly plain, because any object can be interpreted only in terms of another.

Now in our comparisons we find that characters may have different values as expressions of phylogeny, for some can be relied upon more than others to exhibit homologies. We have therefore to work out the relative value of characters.

Just because morphological characters have such varying values as guides in the tracking of racial descent, it would be wholly erroneous to consider them as even approximately equivalent: wrong to simply balance the total number of likenesses against the sum of the differences. This is the mistake made by Eisig (1887): he attempted to ascertain relationships of genera by determining for each the number of characters it has in common with the others, judging the one with the greatest number of such characters as closest to the ancestral stock, and the one with the fewest as the farthest separated from it.

Some characters are less liable to modification than others, are more conservative in their evolution. Others are highly subject to change. These are known to taxonomists as primary and secondary characters, respectively.

A relatively exact comparison can be made only upon the basis of a common corresponding character. Thus we cannot formulate ideas of one animal upon the presence of certain characters that are lacking in another with which we are seeking to compare it.

So comes the principle of comparison; the relative values of characters must be determined before correct comparisons can be drawn. That character is of the greatest value,

most serviceable in the comparison of different forms, which is most conservative and maintains itself with the least modification during racial descent. Thus conservatism comes to be the criterion of homological value. Only by extensive and comprehensive examinations can the relative conservatism of characters be measured. A character that is conservative is one found with little modification in remote organisms; it is the longest guiding thread to mark the way, the path which leads us back farthest into racial ancestry. One character of this kind may be worth more than several that are less conservative. But while we grant it greater importance, we should never rely upon it exclusively. For all characters of any one stage, the characters of all stages, in short, all the characters of the whole ontogeny, must be considered because each has a value as a property of the organism.

In juxtaposition with this principle comes up another. In the comparison of two groups, and particularly when they are comprehensive ones, we have not only to estimate the values of their common characters, but have also to decide the relative phylogenetic worths of the members within each group. This is to be determined after the settlement of character values. For in a race of organisms some are more central than others, which are more extreme; we speak loosely of the former as more generalized, and of the latter as more specialized. That form which exhibits the greatest number of conservative characters common to the whole group would probably be the one most primitive or ancestral, hence the one best fitted for comparison with the other group; and it should be compared with a representative of that other group similarly selected. This is quite different from the method of Eisig, criticised above, in that it comprehends only conservative characters in the comparison. And this is not in contradiction with our

principle that all the diverse members of a group should be considered in our concept of it. For just as we should balance all characters, but make use of them according to their relative values, so we should consider all members of a group, but ascribe them different ranks according to their worth in showing racial affinities. Thus if a more primitive central form has given rise to a diverging constellation of species, and if some of these have departed widely in their properties from the mother form, they are clearly of less importance to the phylogenist than the latter. It is all a question of relative degree of importance; and this must always be determined first, for organisms as well as for their separate characters.

If this is true both for members of groups and for their particular characters, would it also be true of their ontogenetic stages? Are all stages of the individual development equivalent as bases of comparison?

F. RELATIVE VALUES OF ONTOGENETIC STAGES

We have repeatedly pointed out that an organism is no more ancestrally-repetitive in its earlier stages than in its later ones. Therefore earlier conditions, as cleavage or larval form or metamorphosis, can furnish clues to descent in no greater degree than later stages. But while the organism remains one and the same species during the whole embryogeny, the species being fixed as much in the egg as in the adult, some stages are nevertheless more valuable for purposes of comparison than others, in that they exhibit greater amount of perceptible differentiation. We can deal observationally with only such characters as are perceptible, and until we can perceive specific differences in eggs as easily as in adults, the latter are more serviceable objects for study. From the results of present and past experience we are almost justified in the conclusion, that differ-

ences will never be as perceptible in the egg cell stages as in the mature ones. For the ontogeny appears as a progress leading towards increase of perceptible specialization, and if this progress advances continuously towards greater observable specialization, it is obvious that the later the stage in the ontogeny, the greater its importance as a basis for comparison. This would not be so were the perceptible complexity of the egg cell and other early stages as great as that of later stages, but it is not. It is for this practical reason alone that the mature stage is the relatively most important as a basis for comparisons.

This brings up the old discussion of the value of embryological *versus* comparative anatomical evidence. Really the whole morphological treatment of racial descent is of the nature of comparative anatomy, when relatively correspondent stages are compared. The kinds of comparisons instituted between eggs, or embryos or larvae are as much comparative anatomical as comparisons between adult stages. All comparisons in the morphological study of racial descent, when correctly made, are comparisons of anatomy. So there is only an arbitrary line of distinction drawn between embryology and comparative anatomy. Strictly embryological would be only such considerations as those which concern relations of the stages and characters in one ontogeny, without reference to the ontogenies of other organisms.

In species that develop in their earlier stages progressively, then in their later ones regressively, become apparently simpler, are found states where the adult is not the most complex. Such examples are furnished by pronounced endoparasites, such as *Sacculina*. With a knowledge of only the adult female structure *Sacculina* could not in any way be regarded as a Crustacean, for it is a sac produced into digestive branches, lacking almost all the

structures characteristic of a Crustacean. Yet certain of its embryonic stages show marked correspondences to similar stages of undoubted Crustacea. This has sometimes been taken as a case in proof of the idea that the earlier stages of the embryology are fully as important as later ones in determining relationships.

But how should our interpretation of *Sacculina* proceed? Clearly its adult stage shows no important similarities to the mature stages of any true Crustacean; therefore in this stage it cannot be ranked as a Crustacean, the general opinion to the contrary notwithstanding. Its larval resemblances to the larvae of true Crustacea may be interpreted, perhaps, as probable proofs of its derivation from Crustacea, but not as proofs that it is any longer a Crustacean. Likenesses present in earlier stages, but not in later ones, may suggest whence a species has descended, but demonstrate at the same time that it can no longer be ranked with the group from which it was derived. It is strange that this point has been so generally misunderstood. Because a Man has at an early embryonic period evident gill arches and a two-chambered heart, renders the interpretation probable that he had originated from piscine ancestors, but such structures do not show him to be now a Fish. For the same reason the group of the Chordata is methodically inadmissible. It is an artificial association of Enteropneusta. Tunicates, *Amphioxus* and Vertebrates, defined almost entirely upon certain resemblances in the early development first pointed out by Spencer (1865) and Kowalevsky (1866). Total disregard is given to the almost unbridgable differences of the adult stages. If all these embryonic resemblances of notochord and visceral arch formation, origin of the medullary tube, etc., were demonstrated to be close correspondences, which is far from being the case, they would prove no more than that these

groups far back in ancestral darkness may be found to meet. But to associate adult Sharks, Ascidians, and Balanoglossi as members of a common group has no better reason than to combine Men and Earthworms.

Because the adult stage represents the termination of the ontogeny, the end for which the preceding stages are in great measure but a preparation, it indicates better than any other stage the relative phylogenetic rank of the species. In progressive ontogenies its value for comparison is greatest because there it shows more perceptible specialization than any other stage; in regressive transmutation it is equally with the preceding cases of use in determining relative rank, but not of so much importance for deciding racial descent. Secondary racial modifications must affect every stage of the embryogeny. They may arise in any stage of the embryogeny, but when inherited must affect every stage. Therefore any stage should be equally conservative or equally modified. But since all the stages are but a progress towards the adult one, it is clear that this stage more openly than any other should exhibit the scale of organization of its possessor, because in most cases the number of perceptible structural characters is then greatest.

This does not mean that the embryogeny is a change from the simple or generalized to the complex or specialized, for that idea seems to me to misrepresent the phenomena of growth; but rather a progress towards greater perceptible specialization. And that is why different embryonic stages have different values in the practical analysis of phylogeny, and why of all of them the mature stages are in the majority of cases the most serviceable.

We might state this conclusion in another form. All embryonic stages are of value in determining racial descent, but the adult stage is the most important for showing de-

gree of relationship, since it alone exhibits the definitive amount of specialization.

More than this, since the mature stage is the end of the cycle, the goal towards which the other stages are steps, it may become a standard by which to judge the worth that the other stages have for purposes of comparison; that is, become a criterion of what is more primitive and what more secondary in the phenomena of those earlier stages. That would perhaps be primitive in the earlier stages which is in direct line of progress towards the adult condition, and that secondary which is a deviation from this straight course, for the reason that direct progress of the ontogeny is more simple and, other things being equal, more primitive. This last consideration is offered merely tentatively, however, as a suggestion that requires to be tested. Certainly any criterion of what is primary and what secondary in characters should be welcomed, if it has a logical foundation.

On the other hand the earlier embryonic stages are clearly explanatory of the adult one, because they illustrate its formation and elucidate the genetic and functional relations of its parts. This is the great reason for the examination and comparison of the changes before maturity. The ontogeny shows how all the parts of the adult become so disposed and differentiated, but not why. The reason why of the whole process is the bringing about of the adult.

All stages of the embryogeny should be studied, no one of them omitted, in the analysis of racial descent. But they are not all of equivalent value, and the consummation of all the stages, the adult condition, is of the most importance to the phylogenetist. It does not necessarily follow from this that stages nearer the mature one would have greater values for comparison than those further removed from it, however likely this may appear from a mere logical standpoint. For in one organism particular stages may and

probably do have homological worths different from corresponding stages of another organism. The relative value of the stages must be adjudged for each ontogeny by itself.

G. GENERAL REFLECTIONS

The foregoing is a brief exposition of what I would regard as the most important principles in the making of morphological comparisons with a view to analyzing racial descent. They are: the principle of comparing whole ontogenies; the principle of comparing corresponding stages only, when the comparison proceeds to details; the principle of comparison by the synthetic method; and the principle of first estimating the relative value of characters, of embryonic stages, and of members of a group, with regard to their degrees of conservatism. These principles have been formulated and explained because there can be no sure progress in the study of phylogeny without a generally consistent method of comparison. The basic idea is to neglect nothing, to consider every property, kind of individual, every embryonic stage, to do so synthetically, but to judge the worth of each according to its degree of conservatism. In any and every natural science the correctness of the method is the direct criterion of the soundness of the interpretations.

Beyond the principle that only stages correspondent in the same way within their respective cycles should be compared, these principles are not new, and numerous workers have been actuated by one or the other of them. It would be very difficult to trace them all back to their first enunciators, for they seem to have originated independently in different minds and at different times. But it has been only rarely that any one of them has been followed consistently; and there can be no doubt that the majority of "system-makers" have troubled themselves not at all

about broader methods of comparison. The method of classifying upon the basis of a single character is still the one most in use. And there are still morphologists, even among men of influence, who hold that there must be a conflict between anatomy and embryology, and that the results of the two can be combined only by the use of the greatest caution! Only a little reflection is necessary to prove that anatomy and embryology are but distinctions of convenience, and that their subject matter, in so far as it bears upon racial descent, is really one and the same. Yet embryological classifications have arisen to offset anatomical ones, and strange bitterness has grown where there should be collegial harmony. One finds evidence of this almost everywhere, so in the literature on the origin of Vertebrate limbs, of the tracheal system of Insects, of the mouth parts in the Myriapoda, of compound faceted eyes, and of the broad relationships of many groups.

All this conflict has arisen wholly and entirely in confusion of method, not at all in the nature of the observational basis; disagreement has been occasioned by one-sidedness, by the failure to conscientiously balance up and weigh all the characters. And how well this is illustrated by the many hypotheses regarding the origin of the Vertebrates! We can say of them in general that each proponent of a view started with the investigation of some Invertebrate group; being a Vertebrate himself, he naturally acquired interest in his own genealogy and wished to trace it far back of the Garden of Paradise; and consequently he sought for his Adam among the group he knew best. All such work is humanly natural, of great mental interest even, like the ideas of the Rosicrucians; but the method of most of it is quite wrong, and its value on that account but fleeting. Just this is what has caused some good workers to abandon the paths of phylogeny, and to

seek other pastures; yet without reason, for they had but to reconsider their working methods.

Still another hindrance has lingered to this late date to block the progress of a rational phylogeny. Many men who accept the idea of transmutation of species, and so ought to fully recognize that the main aim of phylogeny is the analysis of the phenomena of racial change, nevertheless confuse phylogeny with methods of museum arrangement. They "classify specimens" not so crudely but yet in much the same way as their predecessors of a century and a half ago, in making use of only such characters as require the least amount of investigation. They search for differences by which each specimen may be conveniently assigned to a particular place in the museum collection, and regard that system as the best which can be most readily turned into a key for identification. One may glance over many a modern piece of supposed phylogenetic research, and find it vitiated by this method; yet its authors would indignantly repudiate the imputation. Such a method has its use for the rapid survey of species differences, but it is useless as a contribution to the study of descent.

In conclusion I would quote a portion of the statements upon morphological methods given by Max Fürbringer, in a work that stands among the best and most monumental of morphological monographs, his researches upon the anatomy and taxonomy of Birds (1888). My own conclusions were reached before I had compared his opinions. Fürbringer writes: "The first and most important rule with every work aiming at systematic purposes is: neglect nothing!" Then he says there should be made "a critical estimation of the value of the separate characters. . . . General rules do not admit of *à priori* foundation; but it is good advice, much and accurately to observe and to be guided by the results of more comprehensive researches.

. . . Through the comparison of large series of more closely and more remotely connected forms can the value of the different characters be judged. . . . No character can suffice for everything. . . . The main point is that one lets himself be guided by positive instances, considers the quality and the genetic significance in the first place, does not limit himself to characters that are too localized, and above all, that one brings into the reckoning right many good characters. . . . Should one construct an avian system based on each particular character and then combine all these systems, somewhat in Galtonian manner, one would surely not get a natural system but a bad and useless caricature."

CHAPTER IX

THE RELATIVE VALUES OF MORPHOLOGICAL CHARACTERS

It was one of the principles pointed out in the preceding chapter, that though all characters of every portion of the ontogeny should be considered, yet some of these characters are of relatively greater importance for the determination of descent than others; and that therefore there is a necessity of estimating such values. And it will be recalled that we say a character is of high value in direct ratio to the degree in which it indicates racial descent.

So now we shall treat briefly those morphological properties of animals that are available to investigation, and endeavor to decide which kinds of them are of the most worth.

A. KINDS OF CHARACTERS

A character is simply a property or attribute of an organism. It is then logically incorrect to speak of "negative" characters; to say, for instance, that it is a character of modern Birds to be without teeth in the adult stage. The correct statement would be: these Birds are characterized by a horny covering to the jaws. Frequently one reads that such or such a group, as, *e. g.*, the Mollusca, is definable mostly by negative characters. It may be defined, delimited, from other groups by negative terms, but its characters are all positive, else they would not be properties. On this account there is no occasion for considering the relative values of negative and positive characters, as has so often been done, since a negative character is a contradiction in terms.

Next, it is a tenet of the first importance that we are examining characters to get from them a knowledge of the whole organism; and that we gradually construct a knowledge of the whole as we increase the number of properties studied. If any character be omitted, however trivial, our concept of the whole lacks just in so much. From this it follows that the organism is not a page on which to read a character, but the characters are letters by which to read the organism. No single character, however important, can teach the whole story of the organism, but only a portion of it.

This last consideration leads to the conclusion: those characters are of the relatively greatest value which express most fully the organization as a whole. Previously we had concluded that such characters are most important in determining phylogenies, that are most conservative, least liable to change, during the progress of racial transmutation. Characters that are most fully expressive come to be equivalent, accordingly, to those that are most conservative. And this is not a mere logical quibble, but will be found to be in accordance with the relative values of characters as we understand them. For a character that is most expressive can be only such a one as represents the fundamental structure, hence that structure which has maintained itself during a long past. Other structures arise and disappear, but this one continues, and in so doing is most definitory of both the organism and its past.

Thus fullness of expression and conservatism are the qualities by which to measure the worth of characters. The more characters that are considered, other things being equal, the greater value their combination will have for purposes of comparison, because expressing more of the organism.

Two main sorts of morphological characters may be

distinguished, though in practice both should be conjointly considered.

The one kind are anatomical, characters considered without reference to embryonic change, *i. e.*, characters considered at any point in the ontogeny regardless of their preceding history. Anatomy treats of a character at a particular stage, without comparison with other stages of the same individual. Each stage of the ontogeny can then exhibit anatomical characters, and the latter are by no means restricted to the adult condition. For the examination of two correspondent early ontogenetic stages is as truly comparative anatomy as the comparison of two adult stages.

Three kinds of anatomical characters may be distinguished: quantitative, dispositional, structural. The quantitative characters are relations of number, weight and volume. Dispositional: relations of arrangement, modes of position, relations to particular axes of the body. And structural: all relations of form independent of disposition.

The other main kind of morphological characters may be called organogenetic; they are characters of ontogenetic genesis, of embryonic change. All organogenetic characters express relations of more than a single stage in the embryogeny of one individual; they are founded upon a comparison of such stages.

Organogenetic characters may be regional, temporal, or modal. Regional are those characters of dispositional origin, of position of the first anlagen. Temporal are characters of relative succession, of time of first appearance or specialization; thus it would be a temporal character of the central nervous system to arise before the reproductive organs. And modal are all other organogenetic characters, those of mode or process of formation independent of time or place of origin.

Accordingly, we shall have to consider the following kinds of morphological characters:

<i>Organogenetic</i>	<i>Anatomical</i>
Regional	Quantitative
Temporal	Dispositional
Modal	Structural

B. TEMPORAL ORGANOGENETIC CHARACTERS

It has long been held by embryologists as a fairly justifiable conclusion that organs appear in the embryology in the order of their phylogenetic age, the most fundamental appearing earliest. But while this is more or less true, it is very far from being the rule. It is incorrect to say that organs always appear in the ontogeny in their racial sequence.

In the examples that will be compared to test this point we will mean by first origin of an organ its first perceptible delimitation from other parts of the embryo; but will not consider as its first origin that particular first cleavage cell by the divisions of which its parts arise. Some arbitrary point must be taken as a criterion of first origin, else we could not at all discuss first origins, since all structural parts are ultimately referable to the egg cell. So we will employ the term first origin not in the more precise sense of the cell-lineagists, but in the significance given it by more general embryologists: that of first perceptible differentiation, or what the Germans call the *Anlage*.

Let us consider the succession of the organs in the ontogenies of three molluscs, *Teredo*, *Crepidula* and *Nucula*, from the descriptions given by Hatschek (1880), Conklin (1897) and Drew (1901), respectively.

(a) *Teredo*. (1) Stomodaeum; (2) shell gland; (3) apical nerve plate; (4) velum; (5) proctodaeum; (6) man-

tle; (7) head kidney and otocysts; (8) ganglia, foot, gills.

(b) *Crepidula*. (1) Gastrocoel (mid gut); (2) stomodaeum; (3) apical plate and shell gland; (4) foot, cerebral ganglia, otocysts, cerebro-pedal connectives; (5) head vesicle, velum; (6) external larval kidneys, operculum; (7) right branchial cavity. The specialization of the following takes place considerably later: proctodaeum, gills, permanent kidneys, pericardium and heart, mantle.

(c) *Nucula*. (1) Gastrocoel (the blastopore persists as the mouth); (2) shell gland; (3) test (considered by Drew as equivalent to the velum of other Molluscs, but perhaps more similar to the "serosa" of *Sipunculus*); (4) mantle; (5) anus, cerebral ganglia; (6) liver; (7) foot; (8) pedal and visceral ganglia, otocyst, gills, byssal gland; (9) nerve commissures, labial palps; (10) heart, kidneys.

In these three Molluscs the stomodaeum, shell gland and apical plate are the earliest of the organs to arise; but considerable differences are found in the relative succession of the other organs.

Another brief comparison may be made of the time of appearance of the organs in certain Vertebrates, namely *Amphioxus* (Hatschek, 1881, Lankester and Willey, 1889), Sharks (Balfour, 1878), Frog (Morgan, 1897), and the Chick (Duval, 1889):

(a) *Amphioxus*. (1) Gastrocoel (mid gut); (2) medullary groove, first somite pair; (3) notochord; (4) club-shaped gland; (5) stomodaeum, first branchial slit; (6) opening of ciliated organ (specialization of the left anterior enterocoel; (7) eye, endostyle; (8) proctodaeum; (9) fin.

(b) *Shark*. (1) Gastrocoel, head fold, medullary groove; (2) notochord; (3) first somites; (4) tail lobes; (5) optic vesicle, lens, first visceral cleft, auditory pit, heart; (6)

stomodaeum, cranial nerves, subnotochord; (7) segmental duct, spinal ganglia, liver; (8) thyroid gland; (9) olfactory thickenings; (10) fins, mesonephric tubules; (11) sympathetic ganglia, cloaca; (12) lateral line, pancreas; (13) Müllerian duct.

(c) *Frog*. (1) Gastrocoel; (2) medullary plates, neural plate, notochord; (3) segmental duct, first somites, sense plate, gill plate; (4) optic vesicles, lens, auditory pit, suckers, mouth, anus, liver, heart; (5) gill slits, olfactory pits, brain vesicles.

(d) *Chick*. (1) Gastrocoel; (2) notochord, medullary groove; (3) first somite pair; (4) stomodaeum; (5) differentiation of nervous system into neuromeres and vesicles; (6) vitelline veins, heart, head fold of amnion; (7) optic vesicles; (8) segmental duct; (9) auditory pits, earliest cranial ganglia; (10) lens pit; (11) branchial arches; (12) epiphysis, infundibulum, mesonephric tubules; (13) cerebral hemispheres, olfactory pits; (14) trachea, lungs; (15) allantois and limbs; (16) genital ridge; (17) Müllerian duct.

In all four of these very different Vertebrates the first organ system is the gastrocoel (mid gut); the second the central nervous system with which (in all except *Amphioxus*) the notochord is coincident; and the third (except in *Amphioxus*) the first mesoblastic somites. All these earliest organs are fundamentally characteristic of Vertebrates. The time of appearance of the other organs shows considerable discrepancies, except that the lens pit and the auditory pit always appear very early.

Generally disagreements in the time of succession of parts in related organisms have been interpreted as examples of cenogenetic modification. This has been done notably by Keibel (1895), who has specified various instances of the kind in Vertebrates. But according to our

view a racial modification when inherited must come to influence all parts and all stages of the embryogeny; and therefore it is not correct to speak of certain changes and sequences as cenogenetic and others as palingenetic.

With all the discrepancies in the time of first embryological origin of organs, it is nevertheless the case that the very earliest organs are generally fundamentally characteristic of the group as a whole. So in the Vertebrates the central nervous system and the mid gut uniformly arise very early in the ontogeny. The cavity lined by entoblast cells, the gastrocoel, is in most cases of Vertebrates and probably most if not all other Metazoa, always when the gastrula stage is formed by invagination, the first appearance of an organ, the mid gut. And usually not long after a thickening of the ectoblast marks the beginning of the central nervous system. That there are no other organs for which the same condition obtains, is due to the fact that no other organs are of such general prevalence in animals, with the exception of the outer skin.

Yet right here we notice that the ontogenetic first appearance of one of these organs, when analyzed, does not exactly represent a primitive relation. The first portion of the nervous system to appear in the embryogeny is frequently the central portion, and it is succeeded by nerves and sense organs; thus in the Vertebrates, for instance, the earliest parts go to form the brain tube. But in the racial history the peripheral, superficial nervous system must have been the first stage, and the second the central, coordinating system. For at first there must have been diffused areas of irritability upon the outer surface of the animal, next restriction of these areas to the smaller specialized portions, the sense organs. That is, there must have been coincident development of motor-sensory elements like neuromuscular cells, according to the very

rational theory of Kleinenberg (1872, 1886); next more specialized peripheral sense organs, with wider separation from muscle cells; then afterwards the elaboration of a central nervous system of nerve tracts connecting sense organs and muscles. But in the embryogeny of the Vertebrates this racial succession of the parts is nearly reversed: the central portions arise first. And thus the temporal sequence of the parts in the ontogeny, considered by itself, would give quite an erroneous idea of the racial origin of the nervous system as a whole.

But, though later in racial origin, the central nervous system is in many respects more stabile and conservative than the peripheral; it always persists through all the changes of the sense organs. So the first portion of the nervous system to become perceptible in Vertebrate embryogeny, though not the racially oldest, is nevertheless the most conservative, and on that account most reliable as a basis for phylogenetic inquiry.

And it is much the same with the mid gut. The first ancestral intestine must have had from the start an opening to the exterior. To have been functional from the first it must have arisen as a gradually deepening invagination, like the gastrovascular cavity of Cnidaria. But in the majority of animals, practically all in which the ectoblast grows over the entoblast (epiboly), the gastrocoel has as first no connection with a mouth, but this earliest intestinal portion arises without connection with the exterior. The secondary stomodaeum, which comes to form the definitive mouth and pharynx, is a later differentiation. Thus though the mouth must have been ancestrally the oldest part of the whole alimentary tract, it is the part most subject to change in position, axial relations and time of embryonic appearance; and the mid gut, while a later racial portion, is yet more conservative in the embryogeny.

So in both of these organ systems, the nervous and alimentary, the most conservative portion is the one that arises first in the ontogeny, and not the portion that is racially oldest.

For these reasons the relative time of succession of organs in the ontogeny is to be regarded as a character of some importance in estimating degree of conservatism. It does not present a criterion of homology, but one of relative stability. This is not to be interpreted to mean that organs are to be rated strictly according to their embryonic succession, but that those organs that arise earliest are to be considered highly conservative until reasons are brought to the contrary; not a very precise recommendation, but nevertheless one to be heeded.

Embryogeny examined with reference to external conditions of development teaches that the organism is more or less adapted to, in harmony with, its environment, that it reacts to the surrounding influences during all its stages, and that such reaction power does not open full-flowered first in the adult. That is to say, some if not all of the organs or parts have distinct physiological activities before they have attained their definitive form. Clearly those must develop earliest which first come into use, so that this usage comes to be a very probable factor in determining the time of their first appearance. This suggests that no ontogeny can be properly interpreted without an understanding of the conditions under which the embryo develops. This in no wise presupposes that the factors of differentiation are extrinsic; it simply argues that intrinsic energies must be co-ordinated with external influences. That organ would become perceptibly fully differentiated first that first comes into use; but other organs may appear still earlier in a more undifferentiated condition, whose time of appearance cannot be explained on this usage concept.

Accordingly, relative time of appearance of an organ in the embryogeny would be governed by one of two factors: (1) by its racial age, and (2) by the time when it comes into active employment. If in any case it can be demonstrated that an organ appears very early, without any correlation with early usage, then its precociousness should be attributed to racial conservatism, in which case it would become a character of considerable importance in comparisons. This is equivalent to the current distinction of embryonic characters as adaptive and ancestral, with the limitation that the second kind are of greater importance by virtue of greater degree of conservatism.

C. REGIONAL ORGANOGENETIC CHARACTERS

In the next place we have to consider those organogenetic characters we have called regional.

It is clear that relative position of the first appearance of an organ is to some extent dependent upon the form of the embryo as a whole. So in a flattened embryo, like that of a Shark or Bird, there is at first but one plane, and the earliest beginnings of a paired organ are further apart from each other than is the case in a rounded embryo, as that of a Frog. That is to say, relative position of the halves of paired parts is dependent upon degrees of movement (*e. g.*, concrescence) of the whole. For this reason relative distances of parts right and left from a median axis does not constitute a character by itself, being rather a function of mode of formation. A good case in point is the first development of the heart, which in Vertebrates arises as a paired organ when the cleavage is partial (except in the case of the Shark), but unpaired when the cleavage is total. In such an example the regional appearance of the organ right and left of the mid axis, or within this axis, would

not constitute differences so great as to preclude homology of the heart in both cases.

More important than position to right and left is relative vertical position, and relative antero-posterior position of the first anlagen.

In regard to the last-named relation, considerable differences occur in homologous organs of closely related forms, to some extent dependent upon directions of growth of the embryo as a whole. This is notably the case with the first anlagen of the paired limbs, particularly of the hind limbs in relation to their distance from the end of the tail; relative distance of eye and nostril, and of eye and visceral arches. Yet these relations are on the whole quite conservative, for the liver always develops behind the lungs, the heart in front of the permanent kidney, etc.

The relative vertical position of parts is still more constant. In a Vertebrate the nerve tube always arises above the notochord, and this above the intestine; the somites always at about the level of the nerve tube, and the kidney tubules always at a lower level than the somites. So conservative are these characters of relative vertical arrangement of first anlagen, that they are to be considered of greater homological value than the other regional dispositions mentioned. And in an embryo, as in an adult, we should distinguish not between dorsal and ventral, direction of surfaces of the embryos with reference to the outside world, but between, *e. g.*, neural and haemal (for a Vertebrate), that is, relative vertical position with regard to other parts of the organization. For this reason it is a character of little importance whether an embryonic area forms upon the lower side or the upper side of an egg, according to the position of that egg to the environment; but of great importance whether it has one or another relative position to other embryonic areas or parts.

Cell-lineagists have had much to say about "regional homologies," homologies based upon the positions of the protoblasts of later organs, or upon the positions of organ-forming areas; His (1874) initiated such considerations. These are likenesses in position not of the first perceptible appearance of an organ, but of the earliest cell or region to which that organ can be ascribed. I think that what we have had to say about relative positions of the first perceptible (multicellular) anlages will apply to the matter of earlier relations. In the cleavage of a Mollusc a particular organ has been found to arise from a particular cell of a particular quartette, or from a particular quartette of cells, and this from a particular region of the unsegmented egg. Quartettes are defined not only on relative position, but also upon temporal sequence. In what is known as spiral cleavage, cleavage alternating in direction, considerable changes are brought about in the relative positions of the cells, quite as great and sometimes greater than movements of parts in later stages. On this account simple relative position of one or of a group of cleavage cells to another cleavage cell or group shows considerable inconstancy, is not a character of much conservatism. There is an orderly, determinate shifting of the cells and no irregular movement of them; yet the areal changes of parts in a cleaving egg are on the whole greater than those in the later embryonic history. Accordingly, such organogenetic characters are of little service to the practical phylogenist.

Of all the positions of protoblasts or germ areas, those perhaps are most deserving of consideration that have reference to relative vertical position, just because they are the most constant. We find the case to be very general, for instance, that ectoblast and entoblast are at first at opposite vertical poles, and the mesoblast on either side between these.

D. MODAL ORGANOGENETIC CHARACTERS.

The third set of organogenetic characters are those of mode of formation, so all with the exclusion of the temporal and the regional. It is one of the intensive questions of the day how far such modal processes are mechanical, but into this question we need not enter.

At first thought one would be inclined to believe that the mode of differentiation, the perceptible process, should offer excellent homological characters; that if parts of two organisms develop in the same way they should be considered homologous, and if in different ways, dyshomologous. And this idea is a very general one. But the value of similarity in organogenetic process has been greatly overestimated, as a comparison of modes of formation of thoroughly homologous organs will show us.

The central nervous system in Vertebrates may first develop as a solid chord of cells (Teleosts, Lamprey), or by the closure of an open groove; there are similar differences in the formation of the optic lens, the branches of the liver, and the Müllerian duct. Indeed, delamination frequently takes the place of invagination, or the reverse. Henneguy (1888) pointed out that it is a characteristic of Teleost Fishes, in distinction to other Vertebrates, that most of the organs arise as solid masses rather than as grooves and tubes; yet this in no way suggests that these Fishes cannot be compared with the other forms. The gastrocoel in some animals is open and hollow from the commencement, in others it is a secondary split. The mouth and pharynx in most Vertebrates arise as an unpaired stomodaeum, but in some Bony Fishes they have a paired origin. The proamnion may grow up independently of the posterior amnion, or simultaneously with it; the extent to which mesoblast extends in the first folds of the amnion is very

variable. The embryo may continue at the margin of the germ disc (Shark), or may move near its center (Chick). In Arachnids the embryo may undergo an inversion, or may not. An invaginated entoblast usually remains pushed in, but in some Sponges it may become secondarily outfolded. Limbs may first appear as outfoldings, or as pits that later evaginate. Mesonephric tubules may be from the start tubular, or may become so secondarily. Sometimes a thickening of an epithelium precedes its folding, sometimes not. A multitude of like cases could be attested as evidence of the contention that similarities and differences in such processes as folding, delamination, solid or hollow proliferation, etc., are of very little value in the establishment of homologies, because any one of them is so readily replaced by another.

Or the organogenetic process may be of a histogenetic kind. Thus bones have been sharply distinguished according to the kind of tissue they develop from. W. K. Parker (1868) particularly has insisted upon the value of such differences in determining homologies. He distinguished three kinds of bone formation (ossification): (1) endostosis (now usually called endochondrosis), bone forming in the intercellular substance of hyaline cartilage; (2) ectostosis, bone forming on the inner surface of the perichondrium, around cartilage; and (3) parostosis, "such a bony formation as appears primarily in the skin, in the subcutaneous fibrous mesh, or in the aponeurotic tracts." The primary bones are "preformed" in cartilage, the cartilage preformed in fibrous membrane; secondary bones have only a fibrous preformation. But this histogenetic distinction is not a valid one. Thus the human scapula ossifies from a matrix intermediate in character between cartilage and cellular connective tissue (*cf.* Schultze, 1897, p. 224). Further, any bone that is preformed in cartilage, as the femur,

has, in addition to centers of ossification within the cartilage, peripheral layers added to it and formed from the inner layer of the perichondrium, so by ectostosis. Ectostosis differs histogenetically in no way from parostosis, or what is more frequently called membrane bone formation: in both ossification proceeds from a fibrous tissue. And in the case of parostosis cartilage sometimes arises secondarily.

Such a sharp distinction of primary and secondary bones is then untenable on the basis of histogenesis. Their proper distinction is not this, but difference in time of first appearance, and difference in position: primary bones appearing earlier and in more axial position, secondary bones being more peripheral and arising later. Mode of histogenetic origin of bones is in no way a sure guide to their homologies, despite the rather general idea to the contrary. These homologies must be determined to greatest extent upon their relative positions, particularly in vertical and antero-posterior directions.

All that tissue which arises between the two primary germ layers, and is known by the collective name mesoblast, may be epithelial from the start, may be a solid proliferation, or may at first consist of disassociated cells. This last condition O. and R. Hertwig (1881) called mesenchyme; they limited the word mesoderm to the two others, and maintained that there is such a radical distinction between the two that larger animal groups may be defined on the characters of this middle germ layer, that is, as to whether it is mesenchymal or mesodermal. This was a particularly unhappy conclusion, and but few embryologists have become its adherents. For both methods of formation of this layer may occur in the same organism, and they readily replace each other in related forms.

The process of formation of the mesoblast would seem to be to some extent dependent upon the size of its cells, to

some further extent upon the size and position of the area from which it develops, and to some degree upon the pressure conditions exerted by the bounding primary layers.

But whatever these factors may be, and the cytogenists are coming closer to them than anyone else, the mere mechanical infolding, pole-cell proliferation, delamination or migration of the cells of the mesoblast is so variable, apparently so little conservative, as to offer no good characters for determining homologies. Mesoblast and mesenchyme as distinguished by the Hertwig brothers are ideas of little value, though their theory more than any other awakened interest in the "mesoderm question." We will not go as far as Kleinenberg (1886), and say "there is no mesoderm at all." For the most recent studies have demonstrated that there are two contrasted kinds of mesoblast: the ectomesoblast, formed from ectoblast, and giving rise mainly to larval muscles that may persist up to the adult stage; and coelomesoblast, forming the lining of the body cavity and the musculature of the body wall. A full discussion of these relations can be found particularly in the memoirs of Meyer (1901) and Torrey (1903). Yet this distinction is based upon area of origin, and upon ultimate specialization: it is regional and anatomical rather than modal in character. These are contrasts of greater importance than the essentially modal one maintained by the Hertwigs between their mesoderm and mesenchyme. Consequently the mechanical origin of the middle germ layer has little value for phylogenetic discussion; but its regional origin and ultimate fate may have considerable worth.

No concept of the mesoblast has had a broader and more stimulating effect than that the lining of the body cavity is referable racially to a reproductive sac, this being the gonocoel-theory of Eduard Meyer.

A gland cell is glandular whether it differentiates in a

tissue that was at the start epithelial, as the outer skin, or from one that only secondarily became epithelial, as a pronephric tubule.*

Or an organ of one species may come from an epithelium, that of another from cells that are at first but loosely associated; in illustration is the variety of method of formation of the Amniote ureter, and of the muscle bundles of some lower animals. Tubular structures may develop intercellularly or intracellularly in entirely homologous organs of different organisms, as the intestine in Nematodes, or the nephridia in Annelids. A complex part may be produced after only a few cell divisions, or not until after many, so in the first case be parvicellular, in the second be multicellular; thus the subcuticula (hypodermis) of different species of *Echinorhynchus* may contain only a few nuclei, or a large number of them, quite irrespective of the bodily size of the animal. But for all the species of this genus this cell layer is undoubtedly homologous. The terminal bulb of a Nemertean nephridium is multicellular, while that of a Turbellarian consists of but a single flame-cell; but this should not prevent our regarding these as homologous organs. And it is well known that in closely related species the time of embryonic development of a part, the length of time it takes to reach its finished condition, is subject to considerable differences.

Numerous similar cases could be mentioned to show how little conservative are such organogenetic and histogenetic processes.

There remain to be considered those modes of development which are known as substitution and replacement, as

* I use the term epithelium for any tissue of cells bounding a fluid-containing space, so having a free surface, without consideration of its relation to particular germ layers. In stricter usage "mesothelium" should be applied to such a layer derived from the mesoblast.

addition and subtraction of parts, as metaplasia and cenoplasia. To a dorsal root of a spinal ganglion adjoins itself a ventral root, to the membranous ear labyrinth a bony case, to a kidney tubule a vascular glomerulus; all these are cases of addition. Then there may be subtraction of parts during the organogeny: so the lens of the eye and the auditory vesicle become withdrawn from the lateral line system, the retina from the brain tube, while the greater portion of Meckel's cartilage becomes by absorption lost from the lower jaw and its remaining portion passes into the middle ear. Non-contractile epithelial cells change into muscle, which is a process of remoulding or metaplasia; just as external dermal teeth formations change into plates of bone. In the development of a holometabolic Insect one organ completely disappears, is destroyed by phagocytes, the Huns of the multicellular organism, and a new organ, forming in a different way and perhaps even from different material, comes to take its place; this is replacement or cenoplasia.

Substitution in the development of the individual may be by replacement, by remoulding, or by such a combination of these two processes as is found in the succession of the three kidney systems in an amniote Vertebrate. Metaplasia, remoulding, is usually associated with addition and subtraction, and these three represent a series of processes allied together, but quite distinct from cenoplasia.

Cenoplasia, replacement, is growth probably from reserved building material, as Woltereck (1902) regards it, from living material that has remained relatively undifferentiated. Its essential is discontinuity; while addition, subtraction and metaplasia are processes of more gradual change. In this way cenoplasia becomes a criterion of metagenesis, as we have seen in an earlier chapter. Thus the occurrence of cenoplasia is very valuable in enabling us to decide whether an ontogeny is continuous or discontinu-

ous; indeed it is the only method for this purpose. Otherwise, so far as I see, it has no bearings upon questions of homology.

Metaplasia or remoulding is rich in its suggestion of possible racial substitutions and modifications of parts. But it must be measured with great caution, since embryonic remoulding is probably in many cases different from modification that has taken place in racial genesis. Thus the external dermal skeleton of lower Vertebrates has become to considerable extent replaced in the higher forms by an internal cartilage skeleton. But in the ontogeny of the higher forms the remaining parts of the original dermal skeleton, namely, membrane bones and teeth, arise later than cartilage bones, quite the reverse of their racial succession. So change of position of the mouth during the history of the race must have been gradual, with the mouth always persistent and functional; but in organogeny one embryonic mouth may be formed, then close up, and another arise at a later time. So ontogenetic modes of addition and subtraction and remoulding have their counterparts in phylogenetic change, but the organogenetic ones are by no means accurate measures of the phylogenetic ones.

And now we come to decide which of these various organogenetic characters are of the greatest importance in the estimation of homologies.

Regional characters, those of situation of the earliest perceptible anlagen, are perhaps not of great value, save those of relative position in the antero-posterior and vertical planes. Temporal characters, those of relative time of succession, seem to me on the whole to be of considerable worth, provided that in each case one distinguishes early appearances due to long racial maintenance, from appearances due to early usage of the parts; these can always be distinguished when the life habits during the early ontoge-

netic stages are known. All the earliest of the organs to arise, excluding those developed simply for early temporary use, may be considered as organs of fundamental conservative value, thus highly expressive of the racial past. But the earliest appearing organs of this kind need not have value directly proportionate to the order of their succession. The modal characters, finally, include some of little worth, such as differences of delamination, solid or hollow proliferation, infolding, evagination, migration, etc.; and others of more significance, such as the various modes of substitution. But on the whole the modal characters would appear to have less worth than the other organogenetic characters, because they are the most subject to modification: they throw the most light upon the process of differentiation of the embryo considered by itself, but not upon its racial past.

E. QUANTITATIVE ANATOMICAL CHARACTERS.

Voluminal quantitative characters are of the least value. The old dictum that increase in size goes with advance in racial modification is true only to a limited extent. The largest of the Reptiles may be the most specialized, and this is in general true for the Ammonites. But the most specialized Insects, Gasteropod Molluscs, Birds and Batrachians are certainly not the largest members of their respective groups. Then many Sponges and Cnidaria are larger than many far more complex animals, and some of the Protozoa larger than Rotatorians. Size of the whole organism is clearly not a test of its degree of specialization. To my knowledge no attempt has been made to analyze the factors determining the size of organisms, except in a few special instances.

Relative size of one part to another is of more significance, such as the relative size of the head and the trunk, of an incisor tooth to a canine, of one portion of the brain

to another. Such relative dimensions, however, do not help to explain homologies of organs, but are of use rather in the interpretation of the grade of specialization. Neither absolute nor relative size of the whole or a part bear directly upon any questions of homology.

Numerical quantitative characters are of value also principally in settling degrees of specialization, as when we conclude that diminution in number and progress in concentration sometimes accompany advance in complexity. Yet these have their bearings upon homology, too. For in considering the relation of Annelidan nephridia with Platodan protonephridia, we find as a difference between them that the former are in many instead of a single pair. Then we have to decide: should the Platodan nephridia be compared with but a single pair of those of an Annelid, or with the whole series of pairs? If it could be shown that the latter arose by a subdivision of the former, as we will show to be probable, then the whole nephridial system in the one would be comparable with the whole in the other. This is a fairly well justified interpretation of the relation between the two. In the Nemertean *Stichostemma* I described (1897) how the single excretory duct of each side of the body becomes divided into consecutive portions before the adult condition is attained. And Lang (1881) showed for *Gunda*, a marine Turbellarian, the presence of several pairs of excretory pores. These are actual conditions correspondent to the theoretically demanded intermediate states. But serial repetition of organs constitutes (not initiates) metamerism, and such numerical relations interdigitate with dispositional characters, to which we will now turn.

None of the numerical characters considered by themselves are of any great value, only when considered conjointly with the genesis of the number. And the distinction between the Protozoa and the Metazoa, when it is

rightly conceived, is not one of number of cells, but one of the separation of the germ plasm and the body.

F. DISPOSITIONAL ANATOMICAL CHARACTERS

These have their organogenetic equivalents in what we called regional characters. They are all the arrangements of the parts within the organism, modes of position, and relations to particular axes of the body.

Arrangement of the larger parts appealed very strongly to the older zoologists, who gave them expression in the groups of the Radiata, Articulata, Annulata, Bilateria, etc.; arrangements used very extensively by Haeckel (1866) and continuing into the present time in Hatschek's (1888) groups of the Homaxonia and Heteraxonia. Thus such characteristics have been employed as anaxonic (protean), homaxonic, monaxonic; radial, bilateral, metameric. And other relations of the parts have been established though not distinctly named, such as the relation of dorsal to ventral, of anterior to posterior, of distribution in one or in more than one plane.

In the same organism various combinations of these symmetries and dispositions may be seen. In a Starfish there is a central disc with arms extending out radially from it. But the stone canal and the madreporite plate mar the apparent perfect radially, for they are not even accurately interradial; one can draw an imaginary vertical plane from the center of the disc out through the mid-axis of one of the arms, and find a bilateral arrangement of the parts with reference to that plane. Within each arm most parts are bilaterally arranged, and some of the parts show serial (but not metameric) arrangement, as the lobes of the hepatic caeca. Finally, there is a distinction of an oral and aboral surface; the center of the former can be called the anterior end, and of the aboral side, the posterior. Then a

typically metameric animal, such as a Centipede, shows radiality in the terminal segments of the body; while each other of its metameres, like the antimeres of the Starfish, is bilateral and with dorso-ventral symmetry.

These illustrations are given simply to prove that different plans of structure are by no means mutually exclusive, since they occur in the same organism. The hydroid Polyp is radial; the Scyphopolyp is bilateral on comparison with it, simply by extension of a cross axis of the body. By such a slight change as a circular outline becoming an oval one, one kind of symmetry passes into another. The egg of a Sea-urchin has its substances serially arranged; the *Pluteus* larva that develops from it is mainly bilateral; the adult is mainly radial. In certain Sea-urchins (Clypeastridae) the axes are so modified that the adult should be called bilateral rather than radial; and forms are known which bridge over these two plans. Or a larva may be radial and the adult bilateral and metameric.

One indeed becomes inclined to say with Kleinenberg (1886), "ich bin kein Axenzoologe"!

An exactly radial animal is not known, for even in a Heliozoan the nucleus lies excentric, being misplaced by the central corpuscle. Bilateral symmetry can be established for any organism, by taking an imaginary plane from the center or central axis through a radius of the body; and it is really a matter of taste whether we speak of radiality or bilaterality. All animals of more or less fixed form are, strictly speaking, bilateral with more or less radiality of some of the parts. Or a bilateral animal could be regarded as two-rayed, usually with the two rays apposed and parallel, but sometimes opposite as in a Ctenophore. Our ciliary muscles are radial to the pupil of the eye, the fingers to the wrist; the bronchioles of the lungs are radial subdivisions of the larger bronchi—the bronchial tree is in a

sense as truly radial as a rooted vegetable; most of our parts are bilateral, some metameric. What, then, is the human symmetry?

There is no need of carrying out such comparisons any further. It must be obvious to every comparative anatomist that relations of bilaterality and radially are of exceeding small degree of conservatism. In our interpretations of living, plastic animals we have come too much to regard them as crystals, and have almost sought to apply the terms of the mineralogist. But the parts of an organism do not crystallize and come together along definite planes, according to laws of cleavage and incidence. There is no sharp distinction between the radial and the bilateral type.

Plans of arrangement of the parts were the bases of the classifications of Von Baer and Cuvier. The opportunity for the satisfactory determination of the relationships of groups of lower animals was first given when von Siebold, but particularly the master mind Leuckart (1848), opened the cage of the Radiata, and manumitted that most unhappy family. Yet it is truly surprising with what tenacity mere axial characters still persist in modern discussions, and men who know better argue of the radial and bilateral as things that are unreconcilable. If any anatomical relations are subject to change with mode of life, it is just these, as notably Lang (1888) has pointed out. Of all anatomical characters those of bilaterality and radially are perhaps of the least value.

Because as we have argued the earliest organisms led a creeping life, perhaps upon the sea bottom, and because this kind of life is always associated with elongation of the body and consequent bilaterality, it is probable that radial symmetry is a secondary modification of the bilateral and not primitive.

Jennings (1903) has called attention to a third kind of

symmetry. "This is what in general may be characterized as a spiral type of structure, or at least as a one-sided, unsymmetrical type. This type of structure is found in organisms which move in such a way that no two sides have the same relation to the environment. Movement of this sort is found in those organisms which swim in a spiral course." And Jennings gives a lucid exposition to show how "the spiral course may be considered as a very simple device to enable an organism to make progress in a given direction through the free water without fulfilling the difficult conditions of making all sides identically alike, or of making the differences exactly balance each other." He speaks of the numerous instances of spiral structure in the Protozoa, seems to regard it as the primitive plan in this group, the one from which bilaterality had been derived by creeping locomotion and radially by sessile mode of life. The Rotatoria are mostly bilateral, but in one family of them, the Rattulidae, he shows "we have a group of animals, fundamentally bilateral, which are taking on the spiral, unsymmetrical form as an adaptation to their mode of movement." And he explains the spiral form in general as a direct outcome of the kind of locomotion and reaction.

But though there is in this way a good physiological difference between the spiral and the radial or the bilateral type, there is no good anatomical difference. For a bilateral animal usually has its parts mainly in one plane, and if this plane become twisted, even ever so slightly, it has become spiral. Equally a radial animal can become spiral. A *Planaria* bending to right itself after being placed upon its back becomes temporarily spiral. There can be spiral symmetry of organs also, as the spiral valve in the intestine of a Shark, the cochlea of the ear or the festooning of a turbinal bone, the chistoneury of a Gasteropod, etc. But spiral symmetry has no greater morphological value than

bilateral or radial, and all of these may practically be disregarded by him who is seeking conservative characters.

Much more important than any of the preceding dispositions is degree of concentration of the parts of an organ or a particular region of the body. Dana (1863) was one of the first to draw attention to this, in his ideas of cephalization: the functional and structural antithesis of head and trunk, with the greatest centering of "growth force" in the former, accompanied by concentration there of the more important organs. One particular case he had in mind was the increasing complexity of the head by the addition to it of trunk segments. Another case would be the germinal epithelium, first comprising a wide area of the peritoneum, then becoming restricted to a small portion of it. The parts of any single organ equally may be diffuse, or may be concentrated. The degree of close localization of similar parts of an organ or region, hence their degree of fusion, is of great importance in determining racial advancement, and in practical application must be used in combination with the structural character of degree of specialization of the parts.

But probably the most important of all anatomical characters, because most conservative and so most reliable in determining homologies, is relative position of organs or their parts in antero-posterior and vertical direction. So on analysis one finds that these furnish the most fundamental bases for comparison of *e. g.* the cranial bones: the parietal bone is defined as lying behind the frontal and in front of the supraoccipital, and the opisthotic as lying behind the other elements of the petrosal. Equally, homologies of bones and muscles are determined most positively by their relative positions, vertical or antero-posterior, to certain nerves. All these are characters of relative positions of parts, not of the arrangement of the whole. Such

relative position Owen (1846, 1848) regarded as of the most decisive homological importance; and there can be no doubt of the correctness of his conclusion. In a radial animal there should be considered relative longitudinal disposition of parts in each antimere, as well as relative dorso-ventral position in any antimere and in the central disc or calyx; in a bilateral animal longitudinal disposition, and also dorso-ventral. Whatever the general form of the whole organism may be, and that is a character of little significance, and however much its habits may change, the relative arrangement of its parts in these two directions remains very constant, and just for this reason correspondence of the parts of two organisms in these points is an excellent homological character.

We will not go as far as Owen and say that such arrangement is the only sure criterion of homology; but we will say that of all anatomical characteristics it is the most important and reliable.

G. METAMERIC DISPOSITION OF PARTS

There is one dispositional character, serial repetition or segmentation of parts, that should be considered by itself, because it necessitates a consideration of both embryology and anatomy. And I feel that an apology is due to the reader for such a short presentation and discussion of a subject on which there has been so much controversy. It is like taking a very small brush to paint a very large canvas.

One of the oldest views regarded a segmented or metameric animal as a linear chain of individuals, a series of buds formed asexually but remaining in permanent contact. This corm-theory, as it is called, was put forward by Haeckel (1868), and has been elaborated particularly by Gegenbaur (1870) and Hatschek (1888).

Very serious objections have been urged against this

theory. In the first place a metameric animal, an Articulata, has a most anterior segment, the prosoma or preoral segment, and a most posterior one, the pygidium or telson, which differ in structure and embryonic formation markedly from the intervening segments or metameres. Thus the prosoma acquires its coelomic cavities only secondarily and from the contiguous metamere, it contains supraoesophageal ganglia not found in the other segments, a greater number of specialized sense organs, longer persistence of the larval ectomesoblast, its nephridia develop and disappear early, and it has no reproductive organs. The telson differs in structure notably from the prosoma, is antipolar to it, but equally lacks reproductive organs and nephridia, and has a growth formation quite different from the metameres proper. Hatschek himself saw that this was not in harmony with the corm-theory, for if the metameres were buds, it is not apparent why the foremost of them should differ so much in structure from the prosoma, and the most posterior from the telson. Racoviza (1896) and Lang (1903) have also argued for the unreconcilability of these phenomena with the corm-theory.

Again in true linear asexual budding, in such cases where the buds become actually cut off and become independent individuals, each bud gives rise to the next following, consequently the most anterior is the first formed, and the most posterior the last. And this holds true even though the process may be complicated by the occurrence of secondary and tertiary buds, intercalations, as in some Naiidae. But this is not the succession of formation of metameres in an Articulata. For the prosoma takes no part in the formation of metameres, but these are divided off in succession from the anterior end of the telson. Prosoma and telson, the two ends of the whole body, are of approximately the same age, and not extremes of a graduated series; the portions,

metameres, in between them are the youngest portions of the body. This important objection has been urged by Eduard Meyer (1890).

Then Plate (1901) has reasoned as another objection that the continuance together of a chain of buds would defeat the most important object of budding, namely, increase in number of reproductive individuals and dispersal of them over a larger area. "For the number of the produced eggs it is the same, whether the gonads of a mother animal lie in a chain or are distributed over different individuals. But the number of the descendants would become essentially increased by the chain breaking into many individuals, swimming about independently, which spread themselves over a larger area, for then fewer animals would be eliminated through the struggle for existence. . . . The segmentation of the Annelids can therefore not have arisen through degeneration of asexual division, for the latter is an adaptation for increasing the number of the descendants; for by the hindrance of the separation of the daughter animals that advantage would become more or less removed."

Then Lang (1903) points out that the young stages (larvae) of Annelids and Crustacea in being mostly free-swimming organisms, and not sedentary ones, would be the least liable to give rise to chains of asexual buds, because such a process is essentially characteristic of sedentary forms. *Salpa* appears to be an exception, but we have remarked that *Salpa* may not have been primitively pelagic, but like most other Tunicates have been originally benthonic.

To these objections we may add two others. Why should metameres of Articulates be considered buds any more than antimeres of Radiates? And second, while asexual generation by budding or fission is not infrequent in metameric animals, it is never a single metamere that is cut off, but

always a larger complex, that is to say, in no metameric organisms do any of the segments behave like true buds, for they never become separated from one another singly. All these objections, with another one to be brought out later, render very improbable and unsatisfactory the interpretation of metamerism as a state of asexually produced buds. And certainly there is no good reason whatsoever to consider that in any ancestor of a metameric animal the metameres ever became entirely divided off from one another in linear succession.

Another explanation of metamerism is that of Sedgwick (1884). He proceeds from the assumption that all the higher animals have arisen from Coral-like ancestors. Mouth and anus are regarded by him as derived from a common gastrovascular opening, by slit-like elongation and then closure of the middle portion. This extension of the gastrovascular aperture was held to accompany elongation of the body in the same direction; so that the original nerve ring would become a pair of parallel nerve chords, their portion encircling the mouth remaining as the oesophageal commissure. The gastrovascular compartments of the ancestor are supposed to have become cut off from the intestinal cavity to form the coelomic sacs, and, on account of the lengthening of the body, to have taken up a metameric instead of a radial disposition.

To the credit of Sedgwick's theory is its simplicity, a radial animal by elongation in one axis becoming bilateral and segmented. As a first objection to it may be considered the incorrectness of considering animals like the Corals as even relatively primitive, for structurally they appear exceedingly specialized. As a second objection is the point that in the higher Metazoa mouth and anus are not both differentiations of a common slit-shaped aperture, but at least one of them is a new formation, and they do not develope

in any immediate connection. On analysis, however, this theory appears to be mainly a mechanical explanation of the origin of a bilateral from a radial organism, and from this standpoint no one can dispute its reasonableness. Its direct bearing upon the question of serial repetition is that concerning the ultimate disposition and fate of the gastrovascular branches. Its correctness then depends upon whether the coelomic sacs of the segmented animals have been derived from intestinal outgrowths. The now prevalent view is that such derivation is not probable, but that the coelomic sacs are referable to gonadal pouches.

The earlier view of Hatschek (1886) noted the difference of the anterior part (prosoma) of the Annelid to consist in its originally greater size, and more rapid degree of specialization. "Further there appears the phenomenon that the growth of the trunk is no equal but a terminal one. While the processes of differentiation begin on its anterior end, on the posterior end new material is furnished by growth for differentiation. . . . When in Bilateria, to which is peculiar a terminal growth and a differentiation of the trunk that advances from in front backwards, the continuously advancing differentiation changes itself into one that proceeds by steps, then is reached the type of metameric animals." But this is no explanation of the problem, not even a clear statement of it, and has been discarded by its author in favor of the corm-theory.

Eduard Meyer (1890) presented a suggestive interpretation. The ancestors of the Annelids, so of metameric forms generally, he supposed to be elongate, non-segmented forms, swimming by undulatory movements. Such forms would have possessed a pair of gonads in the shape of long tubes. As these gonads became periodically swollen with the ripening reproductive products, they would offer a hindrance to free locomotion. Attempts at locomotion would

consequently induce the fragmentation of these organs into two rows of equally large serial portions; and the dorso-ventral musculature in particular would have been the most effective mechanical agent leading to this end. Then other organs of the body would come to be grouped around these serial gonads, and so a complete internal metamerism be produced. And Meyer proceeds: "By gradual increase in strength and fixity of the skin, perhaps directly by secretion of a merely elastic cuticula and further also in consequence of the sinuous swimming movements, there formed themselves on the surface annular grooves with thinner integumental portions; for these a fully determinate position, namely between two successive pairs of sexual glands, was marked out by the sexual follicles, which extended themselves during their maturity and consequently swelled out the body at regular intervals. In the so demarcated body regions succeeded then one approximately centrally placed pair to greater growth, and thereby rendered superfluous all further homologues in its segment, and the latter gradually came to complete degeneration." This is a consistent and simple mechanical explanation, and we shall have occasion to recur to it.

Lang (1881, 1903) has been the foremost in the attempt to derive true metamerism from such "pseudometamerism" as is expressed in certain Turbellaria, particularly *Gunda*, where there is regular serial repetition of certain organs but without external segmentation. The arrangement of the genital pouches in *Gunda* is most precise and regular; and he argues that the arrangement of these has led to the metamerism of the other parts, so by their pressure to the intestinal diverticula, nerve commissures, excretory pores of the nephridia, etc. Lang first argued that the coelomic sacs of the higher Metazoa have been derived from the intestinal diverticula of Turbellaria;

but he recently discards this view in favor of their origin from genital pouches, and so aligns himself on the side of the gonocoel-theory of Meyer.

We had best clear the ground for discussion of these various views by disregarding any considerations of what was the primitive ancestor of metameric animals, whether a form like the Trochophore larva or not. For we are interested in determining what answer the morphological character of metamerism can give to the problem of this ancestor. We are employing metamerism as an aid in the search of genetic origins, and are not using hypothetical ancestors to help explain the nature and cause of metamerism.

The problem of metamerism is, to my mind, not so much why duplicate organs are arranged in longitudinal series, as why in the same organism parts should be duplicated. Even in the most perfect segmented forms known there are always some organs that are not duplicated; others that are continuous along the length of the body, but with metameric specializations or ramifications along their course; all these in addition to strictly metameric parts, which are serially arranged but separate. Examples of the last are the coelomic sacs and frequently the gonads, usually limbs when present and other external outgrowths, tracheae and nephridia. But the nervous and circulatory systems, the alimentary tract and the body wall are continuous along the length of the animal. The problem focusses mainly upon those organs that are discontinuous, but the organs that are not may help to explain these. Metamerism is expressive of higher degrees of organization, and the logical method of inquiry is then to look for its beginnings among non-metameric forms possessing multiple parts. The gonocoel-theory of Meyer (1901), highly suggestive as it has been in interpreting the phylogenetic significance of the coelomic

sacs and of the mesoblast in general, regarding them as derivations of earlier genital pouches, stops short of being an explanation of the first steps of metamerism, in that it does not explain why there are many pairs of genital pouches. A Nemertine has serially arranged gonads and otherwise no coelomic sacs, so that it is strong evidence for the gonocoel-theory; but what occasioned the multiplicity of these gonads? Meyer's answer is, mode of locomotion.

There are two possible ways by which the presence of multiple organs of the same kind may be explained: (1) by similar organs developing independently of each other in different parts of the whole organization; and (2) by the division of a single organ into parts.

I think that it can be proven that all multiple organs have arisen by division of previously single (or singly paired) organs. A Medusa is radial, its antimeres are but outgrowths or divisions of a central portion, the radial canals of the central gastrovascular cavity, the marginal sense organs and tentacles but specializations of a continuous sensitive area of the ectoderm. In a Starfish the antimeres are not independently formed parts; all of them are equally outgrowths of a common central disc; so the radial ambulacral canals, radial nerves, radial hepatic diverticula, but branches of central circular canals, ring nerves, and central gut; none of them are formed independently of the central portion. Because this holds for the organs named, may it not be true for the gonads which are discontinuously arranged? Or to take the case of a bilateral animal. In *Planaria* there are on either side of the body gastrocoelic diverticula, branches of one central axial organ; terminal tubules of the nephridia, branches of larger ducts; nerve commissures, branches of longitudinal trunks. The vitellaria, yolk glands, of each side of the body all

open into a common duct, are really outgrowths of the latter. And even the numerous testes can be considered as branches of the vas deferens of each side; not that they develop in the modern *Planaria* as such outgrowths, but that in its ancestor a continuous tube was at once testis and vas deferens, that tube persisting as the larger vas deferens, and branches of its wall becoming the smaller vasa deferentia and the testes.

The disassociated paired and unpaired fins of Fishes are held on the basis of the Thacher-Balfour theory, and I think it the most satisfactory explanation, to be but persisting portions, so divisions, of once continuous skin folds. The separated optic lens and auditory vesicle are with equally good reason considered as but portions of an earlier continuous system, the lateral line. The chambers of the heart arise as subdivisions of a single sac. But we may go further than this and say that, in Vertebrates at least, the metameric coelomic sacs arise as subdivisions of a single pair of sacs; for are not these in Vertebrates but dorsal outgrowths, myotomes, of a pair of ventral hypotomes that extend unsegmented (except for the constriction of the diaphragm) the greater length of the trunk? We can think best of such coelomic sacs as but dorsal pockets of a pair of non-segmented ventral sacs. So the spinal ganglia are specialized portions of a firstly continuous neural crest, as the vertebrae of a continuous vertebral anlage. The parapodia of an Annelid are specialized outgrowths of a continuous body wall; the tracheae of an Insect modified ingrowths of the continuous hypodermis.

All these are cases showing discontinuous, multiple organs to be divisions of continuous, single organs; and any comparative anatomist can at will make the list of illustrations much larger. On the other hand I can recall no case where multiple organs can with certainty be demonstrated

to have arisen independently of each other, without the division of a common ancestral organ. Even the contractile vacuoles of Protozoa, when multiple, are more easily explained as division products of one larger vacuole, which is the condition in the more primitive forms, than as entirely separate formations. The beaded shape of the long macronucleus of a *Stentor* in an expression of incipient division, as is the lobular form of the nucleus in *Vorticella*. One might suggest as objections the cases of the males in *Gordius* and *Echinorhynchus*, where there is a large nerve ganglion in the anterior portion of the body and another in the posterior; yet these are connected by nerves, and so may be quite well considered as enlargements of one continuous nervous system.

So we reach the conclusion that multiple organs arise by divisions of originally single ones, that all multiple organs have probably arisen in that way and not by dissociated first origin. This division may be of the nature of a branching, or by increased growth at certain points and cessation of growth at others, least frequently perhaps by direct fragmentation. When multiple parts are arranged in longitudinal series it is a case of metamerism, so far as that particular organ is concerned. There is no reason to regard such division as a process of asexual reproduction, for, in addition to the objections already made to such a view, one organ system may be metameric and another not at all, in one and the same organism, whereas if it were true budding they all should be metameric. Just as one cell gives rise to others by division, so one organ produces others by division; cell division multiplies cells, organ division multiplies organs, and nothing is gained by analogies with the process of asexual budding. We might almost as truly say *omne organum ex organo* as *omnis cellula e cellula*. The oldest condition of organs

would be singularity, the secondary condition, multiplicity. In a radial animal the division products of organs would become radially arranged, in a bilateral animal longitudinally. Longitudinal sequence of like organs constitutes metamerism.

This throws some light upon a special point on which there has been much disagreement of opinion, with regard namely to the homologization of the nephridia of Platodes and Annelids. The former are in a single pair and the latter in many; but there is all good reason to hold that the former are to be compared with the whole series of the latter.

The interpretation of metamerism is to be the explanation of what agencies have effected the division of once continuous organs; this determined, linear arrangement of the parts is easily explained from the form of the animal. The original ancestor of a metameric animal must have been bilateral because all metameric animals are bilateral. This ancestor must then have had some of its organs paired, but not yet subdivided. Segmentation of these paired organs may then well have been initiated, as Meyer conceived it, by peculiarities in locomotion, so in the first place by the displacement of certain dorso-ventral muscle bundles, these then producing constrictions of the other organs. This seems probable because the metameric animals are for the most part freely locomotor and not sedentary. It is probable that the reproductive organs were of the earliest to become segmented, for the reason that they so very generally show such arrangement; in metameric animals where they occur in but a single pair it is probable that this pair is but one of a former series. Should any paired organ of relatively large volume become first serially constricted, then subdivided into so many parts, it is clear that by mechanical pressure it would induce segmentation

of the other parts, as well as lateral branching of such unpaired parts as the intestine.

The explanation of the subdivision of that organ which first becomes metameric must consider both external stimuli and internal reaction. Locomotion, swimming or creeping, by lateral bending of the body is the nearest and simplest explanation. Yet there are many cases where such movement has not produced segmentation. Nematodes are not metameric though of long form and moving by a lashing of the body. A Gordiacean moves through the water in spiral undulations, but while its ovaries possess numerous lateral diverticula, it has no true metamerism. Both of these groups are characterized by a thick external cuticula, which is to some extent elastic but not at all segmented. A Crustacean has also a thick outer skin; but shows true external and internal metamerism. It might be that the Nematodes and Gordiacea acquired their swimming movements after the development of a thick cuticula, the Crustacean before, which would explain consistently the difference in the two; and in that case the Nematodes and Gordiacea would be descendants of non-metameric ancestors, which I think is without question the case.

The alternative to locomotion as the primary factor in segmentation would be segmentation of inner parts independent of external influences. But this alternative is a weak suggestion, for it leaves entirely open the question of what induces that segmentation. All changes in growth energies are reactions to changes in external conditions, at least so far as we can judge from experiments. The nature of the medium and substratum, the necessity of seeking food, the kind of locomotion employed in this operation, would appear to be the nearest factors in the process. Even cell division is not entirely independent of external influence: a cell does not divide until it has reached a cer-

tain stage of metabolism, but this metabolism is dependent upon nutriment derived from without the cell. Complete metamerism is never associated with ciliary or flagellar movement; but with bendings or sinuations of the body whether in swimming or in creeping. It is, in short, associated with locomotion by undular and successive muscular contraction; where this is most pronounced, *ceteris paribus*, there too is the most marked segmentation; the exceptions would be those cases where a hard external cuticula became developed before this kind of locomotion came into use.

What is of importance to the practical phylogenist is that there is no good reason to regard a metameric animal as a chain of individuals. Hence in comparing such a form with one that is not segmented, the whole metameric body is the unit of comparison and not one of its metameres. Therefore it is quite incorrect to compare, as some supporters of the Trochophore-theory do, only the "head" of an Annelid with a whole Rotatorian, because this is a comparison between a part and a whole. Ontogenetically and phylogenetically the Annelid is at first unsegmented; its metameres are but segments of once continuous parts. Equally we can compare the whole leg of an Arachnid with that of a Crustacean or Insect, or even with the parapodium of an Annelid, though the number of joints is quite different.

A further point is that the immediate ancestor of a metameric animal must have been bilaterally symmetrical, and that a radiate to become metameric must first have become bilateral. Metamerism is a relation of such profound character, concerns so many precise dispositions of parts, that it is highly improbable that an animal once segmented should by transmutation become wholly non-metameric. This is one of many considerations that argues

against the Gordiacea being degenerate Annelids. And for the same reason I would be inclined to regard the Molluscs not as descendants of metameric ancestors, but as a group that had never been metameric; their growth of a heavy shell is not sufficient to explain complete suppression of ancestral segmentation. The general opinion of the close relationship of the Molluscs and Annelids is not well founded from the anatomical side, notwithstanding the general opinion to the contrary; the best evidence for such relationship is wholly from agreements in early ontogenetic stages. Of all the dispositional characters linear repetition of parts is one of the most conservative, and when once implanted in the organization is least liable to give place to another, though it readily becomes modified to slight extents. But there is no reason why different phyla should not have acquired metamerism independently, and therefore that metameric animals may not be polyphyletic.

The organization of a Cestode with its subdivision into proglottids is not metamerism, because these proglottids are actually budded off one by one at the posterior end, and the most posterior of them does not differ except in degree of development from the others. The Cestode is a linear corm of individuals of which no single one contains all kinds of organs found in the whole complex: the scolex lacks reproductive organs, the proglottids central nerve ganglia and apparatus for attachment to hosts. Hatschek regards the complex as neither a corm nor an individual, but as a condition intermediate between the two. It might be better expressed by "corm of imperfect individuals." Lang (1888) conceives the Cestode as a strobila, a linear chain of buds like the strobila stage of a Scyphomedusa, with the difference that the buds of the Cestode never become quite complete individuals. Cestodes are probably modified Trematodes, and the unsegmented ones are es-

entially like the Trematodes except for the lack of an intestine. Both frequently show pseudometamerism in repetition of nephridial and nerve commissures, multiplication of suckers (as notably *Stichocotyle*), branching of the vitellaria, etc. But in the case of Cestodes this pseudometameric condition has not led to metamerism but to incomplete strobilation. The Turbellaria are also pseudometameric. If the Annelids arose from such Turbellaria, as on the view of Lang, for which there is much evidence, then in this case pseudometamerism would have led to metamerism. Pseudometamerism is, accordingly, the initial step in both strobilation and metamerism; both have their origin in multiplication of parts by division. But the two are markedly different in that strobilation is a process of asexual reproduction, while metamerism is not.

H. STRUCTURAL ANATOMICAL CHARACTERS

This third kind of anatomical characters includes all those of form independent of disposition. These are relations that have been most drawn into service by morphologists. Yet an analysis shows that few of them are of value apart from dispositional and organogenetic considerations.

Broadly speaking, structural characters are either histological or organological, *i. e.*, with reference to parts of organs or to whole organs. In the strict sense the former can be applied only to the Metazoa, for they alone have multicellular tissues. Yet we speak of organs and their parts in both Metazoa and Protozoa, hence whether the animal be multicellular or unicellular.

Organ is an exceedingly variable concept, incapable of hard definition, though we generally associate with it the idea of a largest part devoted to a particular function or set of co-ordinated functions. Organellum would be a smallest part with a particular function. So the lung is an

organ, and the liver; each of them is a part of a larger whole, the respiratory and alimentary systems respectively; and each may be subdivided into parts to the point of invisibility. It would be futile to attempt any definition of organ and organ system that would obtain for all cases. For convenience we will call that an organ which is generally so named by anatomists, its characters organological; and histological the characters of its layers or walls, whether they be cellular tissues or portions of one and the same cell.

It would be well to stop a moment to consider exactly what the phylogenist means by the terms individual and organism. Phylogeny has to elucidate the transmutation of races, so that its units are those that make up the races, that is, persons or individuals in the usual zoological sense. A unit or individual would be each largest dissassociated organic whole, so a morphological and physiological whole not composing an integral part of a still larger whole. These are the units of a race. The synthetic group of lowest degree would be what we will call an offspring unit, that is, the group of individuals formed in one generation from one parent; a species would be a collection of offspring-units. In the original statement of the cell theory by Schleiden and Schwann each cell was supposed to be an organic unit or individual. Altmann (1894) has regarded parts of a cell, his granula, to be each an individual, therefore each cell a colony of individuals. We have just seen that an Annelid has been considered a chain of individuals. But Whitman (1893) and Sedgwick (1893) have pointed out how cells of a multicellular complex cannot be regarded as individuals, but as parts of one, for under normal conditions they cannot live independent of each other. Then the egg cleaves as a whole, it is a single organization, and the cleavage cells are not separate individuals but separate

parts. And the cells and organs in their reactions, as Jennings (1904) has so clearly reasoned, are not independent, but "the organism reacts as a unit, not as the sum of a number of independently reacting units." This is like the case of water, which has properties of its own quite different from those of the oxygen and hydrogen that compose it. This is what the elder Milne Edwards meant by "correlation of organs," their mutual interaction; and though there is some modern protest against the idea it is nevertheless fundamentally true. It is just this largest dissassociated organic whole that is the unit of the phylogenist; and he studies its parts or organs simply to get an idea of the whole, and should never confuse them with the idea of individual.

The stalk of the Protozoan *Vorticella*, simply regarded as a retractile organ of attachment, is essentially correspondent to the foot of such an Rotatorian as *Floscularia*. The former is a portion of one cell, the latter composed of many cells. The histological character of number of cells is of little significance. The external skin is probably homologous throughout most of the Metazoa, though it may be ciliated or cuticulated, or provided with various other outgrowths. Whether glands are limited to or extend beneath the hypodermis, whether they are unicellular or multicellular, are differences of very little value. Muscle fibrils differ also in being cross-striated or not, but this appears to be mainly a matter of rapidity or intensity of their contraction, and the transverse lines disappear during a prolonged period of rest; this difference would not throw out the homology of the muscular wall of a Crustacean and an Annelid. The frontal bone is homologous in any two Mammals, though it may differ very greatly in the amount of its spongiosity. A nephridial or gland duct may be intercellular or intracellular; this seems to be but dependent

upon the size of the constituent cells and is no good objection to homologization. An optic lens is always a lens, whatever be its degree of transparency, or the number of its fibers.

On the whole, histological structural differences seem to have little conservatism.

Organological characters may be grouped under very few heads; they are anatomical characters of the larger parts known as organs, or of the whole organism. All organs embrace the three dimensions of space, and so may be to some extent defined, but not explained, in geometrical terms. There are properties of the form of the external contour, as spherical, cylindrical, pyramidal, cubical, etc. Of all formal relations these are the least valuable to the phylogenist. Or an organ may be solid or hollow; a pit, groove, tube or projection; flattened in one plane or folded upon itself; a simple expansion, or branched and lobed; it may envelope another or be contained within it (but these are rather dispositional characters); be articulated or not. These few captions include all main kinds of mere formal relations, and the bewildering phenomena of form may so be reduced to a few simple concepts. The relative value of such differences for determining relationship is very small, unless they be combined with dispositional and organogenetic considerations.

Far more important than the preceding formal characters, because more fully expressive of the whole organization, is relative degree of specialization of the parts, the degree to which its parts are structurally different. Its importance is in determining degree of racial progress, as will be shown in the next chapter.

CHAPTER X

CRITERIA OF RACIAL ADVANCEMENT

THE phylogenist has to decide by justifiable methods two main points: first, the genetic relationships of the different animal groups, and second, their relative degrees of advancement or transmutation from the ancestral condition. The first must be ascertained on the basis of homologies, so far as it is considered from the morphological side. The second must be determined by other criteria. One can study racial affinities without giving particular attention to relative phylogenetic rank; but these relationships must be to considerable degree settled before degree of advancement can be decided.

We have noted that the organogenetic character of greatest worth in ascertaining homologies is the one of regional relations of the earliest appearances of organs in antero-posterior and vertical directions, for it is the most conservative of such characters. Time of first appearance is of importance rather in determining degree of conservatism. Mode of growth of parts is of very little constancy, and serviceable to the phylogenist mostly in the discrimination between continuous and discontinuous life cycles. Yet of all characters these modal ones, treating of processes, are of the most value in the analysis of the phenomena of specialization. The anatomical character of most significance for the ascertainment of relationships is not any quantitative one, nor even any character of form or finer structure, but relative disposition of parts. Therefore, it is particularly regional relations, of position of one organ to another in

the embryo and in the adult, that are the decisive ones in questions of homology. And this was the criterion of homology emphasized by Owen.

Quite different are the characters that must serve as criteria of degree of racial advancement from an original ancestor, of what is frequently named "high and low in the scale of development." Here are of the most use organogenetic characters of process or mode of formation, with respect to their degrees of primitiveness, particularly modes of addition and subtraction of parts, and replacement by metaplasia and cenoplasia; anatomical characters of degree of specialization of each part, relative number of parts, and their degrees of concentration.

By racial advancement is meant here degree of morphological departure from an original ancestor. We may assume that all Metazoa are modified descendants of certain common unicellular forms, though this is an unproven premise and predicated merely for the sake of lucidity in the following discussion. Those would be "higher" in the scale of descent which have departed most widely, and those "lower" which have departed less extensively; it is a question of amount of transmutation. And it is obvious that grade of advancement need not be directly proportional to the geological age of a race, for a modern *Amoeba* is far less advanced than a Carboniferous Ammonite.

We have noted that there is no good evidence that descent with modification is determined alone by any innate qualities of the living substance; that there is no pre-determination or perfecting principle in the Nägelian sense. Then it must be recalled that development may be regressive as well as progressive, that the two are by no means exclusive but frequently coincident, in that one part of an organism may progress while another regresses. Increas-

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ing structural complexity would then be a criterion of progressive development alone, not of regressive, and so is but an incomplete measure of racial change. For there can be as much advancement, in the sense in which the term is used here, in regressive as in progressive direction. The development may be forward in an approximately straight line, or it may turn upon itself by the animal progressing up to a certain point, then regressing, as in the cases of internal parasites. The question is then really length of the line of development independent of its direction. It is conceivable that a Protozoan could transmute into a complex Metazoan, then by degeneration become unicellular again; such a case is so unlikely that practically it may be left out of account. Yet should an example of this kind be demonstrated, the end product of such a racial cycle, though structurally as simple as at the start, would nevertheless be far more racially advanced than any Protozoan, and though unicellular be no Protozoan. It is just the same with the case of *Sacculina*, a highly modified parasite which has evidently originated from Crustacea, but has transmuted so widely from them that it cannot in the adult condition be considered a Crustacean. We have to measure racial change by the number of steps in transmutation, counting all steps, both progressive and regressive.

We say an organization is generalized when it shows a number of qualities, not one of which is pre-eminently developed above the others; and specialized, when one particular character is more pronounced than the others to the extent even of producing their suppression. So an egg cell is generalized because it maintains all the inherited qualities of the race, while an adult body cell is specialized by reason of the exclusive development of one. Specialization is in this sense an advance beyond a generalized condi-

tion, and, with respect to the illustration just given, a progressive advance of one character with regressive suppression of the others. In the case of *Ascaris*, Boveri (1887) has demonstrated that the somatic cells become specialized by a process of loss (diminution) of their hereditary substance; and Goldschmidt (1904) has shown that the chromatin so cast out into the cytoplasm becomes there an organ, the chromidial net, that is intimately concerned in specialized metabolism. Thus specialization is in some part at least effected by loss of germ plasma from the nucleus of the cell; and we showed that differentiation during the process of cleavage is perhaps caused by the dislocation of some of this substance into the cell body. An organ is specialized when its structure allows it to perform but one function, as well as when each of its parts can carry out but a particular portion of that labor. This is the general usage of these ideas, not new but nevertheless necessary to understand clearly. Any character which will serve to measure degrees of generalization and specialization will also help in deciding some of the questions of racial advancement. But von Baer's principle that development is a "progress from the generalized to the specialized" was used by him only for the embryonic process, and should we apply to the phylogenetic also we would find it to hold of progression but not necessarily of regression. Therefore degree of specialization is not all sufficient, but must be complemented by other criteria. That is, there must be a measure also of what may be called despecialization, or change from the more specialized to the more generalized.

Of course generalization does not necessarily imply simplicity; for the egg cell is generalized, yet in most cases it is very complex.

Here are two well-known animals, a Leech with thirty-three segments and a Nereid with a much larger number. Is

the higher or the lower number a more advanced condition? These segments are divisions of a body that in the original ancestor was unsegmented; a smaller number might be primitive, or it might be a secondary result. If the smaller number were a regression, it would be probable that segments primitively present had been lost through a process of coalescence or concentration, for certainly they could not have fallen out of the body. If the smaller number were primitive, then a single one of such segments would be correspondent to several of a form with a larger number.

So to attempt to decide this apparently simple question we find ourselves at the outset in a maze of questions concerning concentration and subdivision or diffuseness, intercalation and addition. It would be absurd to conclude that all Articulates with a large number of segments are more advanced, or less advanced, than all with a smaller number; for each case must be worked out by itself with reference to its immediate ancestry, before more distant ancestral conditions can be determined. A greater number of parts is an advance beyond a smaller number, when the greater number has been produced by division of fewer. But a decrease in number, by concentration or by development of the few at the expense of the many, is an advance in specialization. Probably in any progressive racial series there have been the three stages of singularity, multiplicity associated with homogeneity, and secondary paucity combined with heterogeneity—a series that recalls Spencer's definition of life. Such is the succession, for instance, in the teeth of Vertebrates, where one or a few large dermal plates covered the mouth surfaces, these segregated into numerous teeth alike in form, the latter finally became fewer and diversified in form and use. Here the condition of largest number was intermediate in occurrence between the most generalized and the most specialized states; and the

latest condition was produced by suppression in unison with concentration and differentiation.

Thus degree of perceptible complexity, particularly numerical complexity, is far from being a sure criterion of specialization; and small number of parts for a particular function may be a higher condition, concentration being a more advanced condition than separateness. That is one of the reasons why relative arrangement of organs and their parts, particularly degree of intimateness in their connections, is such a valuable criterion of racial change. And it is obvious that organogenetic processes are of great importance in correctly interpreting adult conditions of this kind, for they show concentration at work, though not necessarily in a way parallel to the phylogenetic course.

Diffuseness and separation of parts is a mark of either primitiveness or of regression, and it is often difficult in practice to decide which. But there is one reliable criterion of regressive development: when the adult stage is less complexly specialized than an embryonic stage; and simply because such a condition cannot be explained on any idea but that of degeneration. A sign of degeneration is complete loss of a part without commensurate compensating specialization of another part. For an organism takes a backward step when it suffers loss in one part, without corresponding growth in another. Metaplasia and cenoplasia may be progressive or not, but loss without marked compensation is certainly regressive. A Cestode has lost its intestinal tube, and in compensation has acquired a more porous body wall and greater development of the parenchyme tissue; but the compensation in this case has not been to the extent of greater specialization, therefore the Cestode is more degenerate than its Trematodan ancestor. But the modern Bird has lost two fingers from its hand,

in compensation the remaining ones have become stronger and anchylosed together, the muscle tendons have become longer and stronger, so that this loss has accompanied greater specialization. Yet in many a case it is very difficult to gauge the amount of the compensation.

In estimating racial advancement, just as in determining relationships, such characters should be employed as are at once most conservative and most fully expressive of the organization as a whole.

Amount of perceptible specialization during the embryonic cycle might seem a good criterion of progressive racial advance, on the assumed ground that it would be the greater the greater the amount of ancestral transmutation. Yet this is by no means always the case, for embryonic changes may be lengthened and complicated by adaptations not represented in adult ancestors. The ontogeny is also in no way a repetition of the ancestry. Fitness to environment is also no test, because we should assume that all animals are so fitted as long as they continue to exist. The old dictum of Man as the most fit of all organisms has no biological basis.

When we review the main criteria commonly employed to measure racial advance, to determine what forms are high and what are low, we find no one of them to be of constant value. Complexity of structure is a mark of progressive transmutation only, direct loss without compensation, of regressive; numerical or other quantitative relations must always be analyzed for each case separately. Progression is perhaps more easily demonstrated than regression, because for it we have to determine only degrees of specialization. And the old idea must be combated, that amount of advance of the mental processes is necessarily a mark of racial progression.

Von Baer (1828) touched upon these questions with his

broad and genial mind, but without application of the principle of transmutation. So in one place he presents a fanciful discussion between a Bird and a Man: the former maintaining stoutly, and with good enough reason, his superiority to humanity in the matter of morphological specialization. I have not von Baer's work before me, and cannot repeat from memory his exact statement of the Bird's case. But if we should attempt a comparison of a living volant Bird with such a Mammal as an Opossum, we might well consider the Bird the more advanced organism. The Bird is far more specialized with regard to the ankle-joint and foot, modification of the fore-limb with its suppression of most of the carpalia and the first and fifth fingers, the upright carriage, degree of ankylosis and pneumaticity of the bones, presence of air-sacs and complicated syrinx, replacement of teeth by a horny bill, dilation and complication of the sternum and compensating shortening of the tail, greater complexity of the eye and the alimentary tract, greater development of muscle tendons, possession of complicated feathers, etc. The Opossum is more advanced in having no free coracoid or quadrate, no sclerotic plates upon the eye-ball, reduction of the hyoid bones, in the complete diaphragm, more complicated reproductive organs and development of a perinaeum, and more compact kidneys. In its skeleton, external and internal, the respiratory and alimentary apparatus, the Bird is more specialized; the Opossum particularly in its urogenital organs. The brain of a Sparrow is from various points of view as specialized as that of an Opossum, with relatively larger cerebral hemispheres and greater retardation of the mesencephalon; and the form of its spinal cord more specialized.

Both Bird and Opossum have in common as marks of progression: loss of abdominal ribs and of one aorta, of prepubic, interclavicular and episternal bones, of various

Reptilian cranial bones, of the centralia; presence of a four-chambered heart, and prominence of the fore-brain.

Man is of course more specialized than the Opossum, particularly in the upright carriage with consequent division of labor between hands and feet, loss of the tail, smaller number of teeth, and especially the amount of differentiation of the brain; but in a number of important osteological and splanchnological properties he is less specialized than a Bird. There is a far greater amount of difference between the specialization of a Grasshopper and a Fly than between that of a Man and an Opossum. It is then all a question of whether the points of superiority of a lower Mammal are to be adjudged to outweigh those of a Bird, and such balancing is very difficult. For differences in number and structure indicates sometimes advanced, sometimes primitive, conditions; loss of a part is a progression when accompanied by compensatory growth, otherwise not, etc.

But this comparison was mentioned mainly to call attention to the conclusion, that because one animal group is on the whole more advanced than another, as the Mammals than the Birds, it by no means follows that all the members of the first group are either more advanced or more specialized than all of the other. And there is very good reason to consider the most specialized Birds to be racially more advanced than the most generalized Mammals.

Ideas of relative phylogenetic scale should never be used as working hypotheses in the search for homologies, for they can be positively determined only after homologies have been settled. These two lines of inquiry must be kept distinct. An Echinoderm may be racially more advanced than a Crustacean, or may not be; it is futile to discuss such a case until the phylogeny of each is more fully known, for until it is, we cannot understand the value of the characters which we use as gauges of rank.

Confusion has arisen from the method of starting out with preconceived ideas of scale of advancement, and letting these influence ideas of homology. This is a case of placing the cart before the horse, and consequently progress has been impeded by it. There is no justification in concluding offhand that a Mammal is higher than a Bird, a Ctenophore than a Coral, or an Insect than a Spider. Relationships must first be determined, then on the basis of them interpretations of relative rank.

Nothing is perhaps more difficult than to free one's mind of preconceived ideas on issues that one means to analyze with unbiased judgment. It is indeed impossible to be entirely free from them. They are the heritage from a long past of thinkers, and to understand the scope of a problem one must perforce become acquainted with the earlier expressions of view. Then, too, a preconceived stand in the form of a working hypothesis is really necessary to shape the course of the investigation and argument. But if one hopes to place upon a firm foundation his ideas of racial genesis, to have no flaws in the masonry, he must without fail rid himself of all his earlier opinions concerning the relative rank of organisms in the progression of evolution.

CHAPTER XI

CONCLUDING REFLECTIONS

THERE are certain conclusions that have such fundamental value in any study of racial descent that they should be considered as principles in directing the course of investigation, and it is the purpose of this chapter to recall some of them.

The whole study of phylogeny is necessarily based upon the idea of transmutation or evolution of species. The evidence on which this rests is clear and unmistakable, and is well substantiated. Therefore the first premise is well founded, yet it is an obligation of phylogeny to strengthen and elaborate this foundation.

Consequently, the first working principle is to consider each vital phenomenon as a step in individual or racial change. [The point of view should be to consider all Nature as in motion, and to regard each phenomenon as a part of progress.] The morphological method is really the same as the physiological, when the morphologist regards structure merely as a visible stage of process, and there is no conflict between the two. Therefore it makes little difference whether one tries to analyze progress by investigating directly function and response, or by determining it through comparison of structures. All that bears on the understanding of process, from whatever point of view it has been won, may be of value in the interpretation of racial descent. Phylogeny thus includes all study of living process, and uses it to determine racial descent.

[The second principle is to consider all kinds of phenomena that have any bearing upon process.] Heretofore

our interpretations of descent have been based to great extent upon morphological evidence. That has been an error, but one can well understand that it has come about simply because the phenomena of form have been supposed easier to analyze and clearer to interpret. Whether structure is so readily explained I would much doubt, for the deeper one penetrates it the more perplexing it appears. But however this may be, organisms should be interpreted from all their relations, that is, from much more than the structural. Besides structure we should include in our comparisons all energies of the parts, their chemical and physical constitution, and particularly all their highly complex relations to the environment. None of these should be omitted, because all can be of aid. The point is just this: one must seek all the evidence he can get, and therefore must use all kinds of evidence.

Yet erroneous results would be reached did not we take into consideration a third principle, which is, to determine the relative value of each kind of evidence.⁷ This concerns the method of comparison. Individual mental attitudes may evaluate different series of phenomena differently, so that conflict of opinion is bound to continue, and fortunately, since it adds a zest to the pursuit. But during the institution of comparisons one should constantly reflect, and ask himself "what are the relative values of these characters that I employ to determine kinships?" The only general criterion of the worth of characters is degree of conservatism, and this can be elucidated only during the progress of comparison. But unless one realizes that characters have very disproportionate values, and that nevertheless all characters should be considered, one is not in position to pass upon racial descent. Characters of an organism are its relations, and the more of them one understands, the more fully one comprehends the organism.

A fourth principle is that we should assume essentially monophyletic origin of the known organisms, until the opposite can be proven. For this principle allows us to include all kinds of known organisms in our comparisons. It is as yet only a premise and requires substantiation.

A fifth principle is to anticipate approximately intermediate connectants between species. So far as our knowledge extends at present, racial development takes place in two ways, by continuous change and by discontinuous. The latter, mutative, has been demonstrated in some cases, but even in it the states of sudden change are often very small in amount, particularly in that often only one character mutates at a time. The continuous transmutation shows exact intermediates, and we have brought reasons to show that it may not be rarer than modification by mutation. The method is correct in principle, accordingly, to postulate approximate if not exact intermediates.

Another, sixth, principle appears to me to be well substantiated. It is, to consider modification to be due to response on the part of the organism to a stimulating change in the environment. We are neither to conceive of organisms as passively moulded by the environment, nor yet of them as changing irrespective of it. But we should regard an organism as a complex of energies which will continue to operate without modification until a stimulus from without calls forth a changed response. To consider racial change as actuated by change within organisms irrespective of any external stimuli, would be to postulate that organisms are independent of their environments and are energized solely by some inherent motions. It is a fair statement that the life of an animal or plant consists in response to stimuli; and experimental study is demonstrating that many of these stimuli are external. This principle not only allows us to employ the relations

of organisms to environments, but also emphasizes that there can be no adequate comprehension of animals and plants without an understanding of their environments. It is quite unfounded to maintain that the hereditary substance, germ plasm, differs in this regard from the somatic material. The hereditary substance is not excluded from external influences, and indeed must become affected by them, although perhaps to less degree than other substances. And this suggests that a racial change, an individual modification that becomes inherited, is the consequence of environmental influence affecting the germ plasm.

A seventh principle is that the development of the individual does not recapitulate the development of the race, that no particular ontogenetic stages are more ancestrally reminiscent than others, but that all stages of the ontogeny are equally cenogenetic or palingenetic. This results from the recognition of the mode in which modifications become racial: to become inherited a modification must induce a change in the energies of the germ plasm. Because the latter is continuous from generation to generation, from cell to cell and from person to person, and because it is likely that the individual development is to some extent predetermined by germ plasm energies, it follows that a change in the germ plasm of the egg cell, to become transmitted, must come to engender change in all following ontogenetic stages without omitting any of them. This concept results also from the idea that an individual remains one and the same species through all its changes, and that two species are as distinct in the egg cell stage as in any later one. A new racial modification may arise at any stage of the ontogeny, but in becoming inherited it must produce change in every stage of a succeeding ontogeny.

Attention may be called to still an eighth principle. All

comparisons between diverse organisms are necessarily of the nature of inexact analogies, because they are comparisons of states that are different. In the greater part of phylogenetic research we must base conclusions upon just such inexact analogies, indeed in all cases where descent cannot be experimentally ascertained. The more unlike two organisms are the more difficult it becomes to compare them; the same conclusion obtains equally for comparisons of parts or stages or environmental relations. Those generalizations will be the most securely founded which are based upon the most exact comparisons, or, to put it in other words, where the inferences are the most direct. To minimize the inexactness of the comparison we may gain much by the eighth principle, which is, in the comparisons of any two organisms to compare only relatively correspondent stages. By this correspondence we mean relative position of a stage to the other stages of the ontogeny. Therefore comparison of two 1-cell stages is justified, or comparison of two mature stages, but not of a mature stage of one species with a juvenile condition of another. This principle is a further objection to the use of the recapitulation hypothesis. If rigidly followed, this method of comparing only relatively correspondent stages will insure the greatest possible surety in generalization.

A ninth principle would be this: that the unit of comparison in the analysis of racial descent is the whole individual during its whole life history, and not any arbitrarily selected stage of it.

The preceding appear to me to be the more important ideas that should guide phylogenetic research, and the ones that promise most for the analysis of the phenomena.

In the interpretation of racial descent most students have made two radical errors. The first of them is the adherence

to a limited range of phenomena, with disregard of others that may be equally important, and even if less important should not be neglected. And the second is lack of consistency in methods of comparison. Frequently the same naturalist bases one group on characters of the mature stage only, another group on characters of some younger stage, and still another group upon supposed resemblances of non-correspondent stages. The method must be consistent, whether it is a good or a faulty one. And above all it is necessary to free one's self from biases learned in the schools towards this or that doctrine, and to occupy a new and unprejudiced stand; for the impedimenta of the past have seriously retarded progress.

Another point is evident, that phylogeny and classification are not synonymous. Phylogeny is an analysis of phenomena leading to a causal interpretation of genesis; it is the study of change in the broadest possible sense. Classification is simply an arrangement into groups of organisms whose racial histories have been so determined, an arrangement that is of use in stating a portion of the results of phylogeny in concise form. Phylogeny makes a rational classification possible, but it also does much more in explaining processes.

When one reviews with an honest open-mindedness the scope of the study of phylogeny, its programme, he comes to acknowledge that it is not a pursuit for beginners and dabblers, but one that requires a broad and varied comprehension of vital phenomena. One must have a consistent interpretation of the processes of heredity and differentiation, and of the mode in which variations become inherited. This is a fundamental preliminary. Then a knowledge and understanding of modes of reproduction and of kinds of life cycles and their significance. Yet these phenomena of generation have been unduly neglected by phylogenists.

And quite of equal importance is always to associate in our concept of an organism its conditions of existence. Only within comparatively recent years have men attended to the factors of environmental distribution conjointly with questions of descent. Had more attention been devoted to them many harmful errors might have been avoided, such as the insistence on pelagic life being primitive, and the maintenance of close relationship between the freshwater Rotatoria and the marine Annelid larvae. And together with environmental relations habits should be treated. We have pointed out that the analysis of parasitism may throw considerable light upon descent, and that so may also periodical migrations. For there is an evolution of habits quite as much as of structure, and it may well be that habit is the initiative in organic change.

Valuable as its results have been, paleontology should not be ranked as the most important method of determining descent. It offers as material for comparison little beyond structure, then only a portion of the structure, and further the geological basis of the relative succession of the fossil-bearing strata is far from secure. Paleontology discovers for us connectant forms, and that is its great value; but in all probability it will discover only a small fraction of such forms. Then, also, conclusions based upon astronomy and geology concerning environmental conditions in earlier epochs are as yet insecurely demonstrated and highly conjectural. We should try to analyze the behavior and nature and relations of organisms of the past in the light of thorough and accurate analyses of modern living beings, and thus apply in paleontology the method introduced by Lyell in geology.

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